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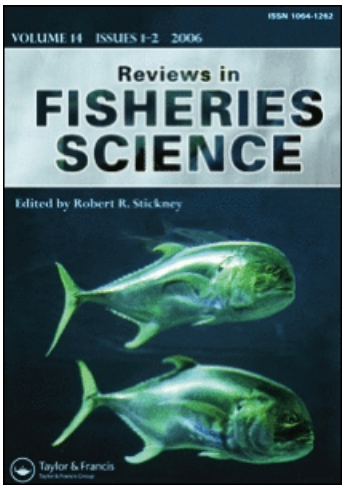

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Ecophys.Fish: A Simulation Model of Fish Growth in Time-Varying Environmental Regimes

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Ecophys.Fish: A Simulation Model of Fish Growth in Time-Varying Environmental Regimes

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Ecophys.Fish is a deterministic STELLA® model for simulating rates of fish growth in environmental regimes that have simultaneous temporal variation in food, oxygen, temperature, pH, and salinity. The purpose of this article is to introduce Ecophys.Fish to those who might want to use it as a framework or starting point for applications of their own. We believe our model, although focused in autecology, will prove useful at organizational levels both below and above the individual fish.

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Ecophys.Fish is a quantitatively explicit interpretation of concepts originally formalized by F.E.J. Fry, almost 60 years ago. Fry's "physiological classification of environment" and his concept of "metabolic scope for activity" were coupled with conventional bioenergetics to provide the model's theoretical basis. The model's inputs are initial size of fish, and time series of temperature, pH, dissolved-oxygen concentration (DO), salinity, and food availability and its energy content. Outputs are food consumption, oxygen consumption, waste production, energy content of fish biomass, and growth. Indirectly, the output is a measure of relative fitness of the fish-environment system to support fish growth.

*Two variants of the model represent the euryhaline red drum (*Sciaenops ocellatus*) and the freshwater bluegill (*Lepomis macrochirus*). Ecophys.Fish had its beginnings in laboratory experiments with juvenile red drum. These experiments enabled definition of functions and their parameterization, leading to a working model that effectively simulated growth of red drum in various pond and estuary trials with caged fish. Subsequently, Ecophys.Fish was converted to simulate growth rates of caged bluegill involved in stream ecoassays. The latter work confirmed the model's generality and the utility of automated routine respirometry for empirically estimating a key model parameter.*

Ecophys.Fish comprises an effective tool for resolving sources of variation in fish growth, even in natural systems with high levels of environmental variability. Moreover, the model has utility for probing biological and ecological mechanisms underlying fish growth and production. Finally, Ecophys.Fish is capable of producing rich hypotheses, e.g., 1) the optimum temperature for growth decreases whenever DO, food availability, or energy density of available food is limiting; 2) with unlimited DO and food availability, the optimum temperature for growth increases *with increasing fish size but only when energy density of food is limiting; and, 3) when neither availability nor energy density of food is limiting, growth can be much faster under diel-cycling regimes of temperature and DO than under the optimum constant temperature/DO regime. Under Ecophys.Fish, environmental regimes that are best for survival are not necessarily those that are best for growth.*

Keywords acclimation, bioenergetics, ecophysiology, F.E.J. Fry, habitat value, metabolism

Introduction

Models of aquatic-system performance typically reflect a top-down view of a steady state world. Here we describe an ecophysiological approach for modeling fish growth in environmental regimes that have simultaneous temporal variation in food, oxygen, temperature, pH, and salinity. We offer this as a step in bringing greater biological realism to the problem of understanding fish performance in habitats characterized by marked environmental heterogeneity in time and space (e.g., estuaries).

Our model incorporates a quantitatively explicit statement of concepts originally formalized by F.E.J. Fry (Fry, 1947, 1971) and subsequently elaborated by Neill and Bryan (1991) and Neill et al. (1994). Fry's "physiological classification of environment" and his concept of "metabolic scope for activity" were coupled with conventional bioenergetics to provide the model's theoretical basis. The model presumes that all of environment acts on animal activity through metabolism, and that these metabolic effects can be resolved into those due to five classes of factors. Controlling factors like temperature and pH set the inherent pace of metabolism. Limiting factors are resources like oxygen and food-energy substrates that, when deficient, restrict maximum or active metabolism. Loading (= masking) factors like extreme salinity and parasites increase obligatory metabolic work; i.e., loading factors increase minimum or standard metabolism. Lethal factors like toxins and

predators kill the animal by completely interdicting its metabolism. Finally, directive factors like chemical gradients and photoperiod guide the animal's enviroregulatory behavior and adaptational physiology. Jointly, the factors of environment determine the animal's metabolic scope, which is the difference between its active (= maximum aerobic) and standard (= obligatory minimum) metabolic rates; metabolic scope, which also has been termed metabolic power (Bryan et al., 1990), is the animal's capacity to perform useful activities like locomotion, feeding, and the physiological processing of food that leads to growth.

Under our ecophysiological model, a fish eats all appropriate food encountered or until available digestive or metabolic capacity becomes insufficient to support the processing of more food. The fish then partitions the consumed food energy and substrates in the usual ways (conventional bioenergetics) between various obligatory activities and growth; if obligatory activities cost more than available metabolic scope, the fish loses mass and energy (but does not die—that irreversible consequence of exposure to adverse environment being reserved for lethal factors). Time-varying environment is accommodated as limiting (oxygen and food), controlling (temperature and pH), and loading (salinity) effects on metabolism and, thus, on metabolic scope. Because the present version of the model lacks explicit treatment of swimming and its metabolic costs, it has been expedient to adopt "Winberg's rule" (Winberg, 1960): Routine metabolism is a constant multiple—nominally, two—of standard metabolism. This leads to functional definition of metabolic scope for growth as the active metabolic rate less twice (nominally) the standard rate.

The conceptual model has been customized for red drum (*Sciaenops ocellatus*) and, with somewhat less confidence, for bluegill (*Lepomis macrochirus*), and implemented in the symbolic systems modeling application STELLA® for simulation (Figure 1). To the simulation model, we have given the name "Ecophys.Fish." Ecophys.Fish had its beginnings in laboratory experiments with juvenile red drum, mostly at Texas A&M; these experiments enabled definition of functions and their parameterization, leading to a working model that accurately simulated growth of red drum caged in coastal ponds and estuaries. Subsequently, Ecophys.Fish was converted with considerable success and minimal restructuring to simulate growth of caged bluegill involved in stream ecoassays. All versions of Ecophys.Fish described here are completely deterministic and have a native time-step of 1 h.

The purpose of this article is to introduce Ecophys.Fish to those who might want to use it as a framework or starting point for applications of their own. Our purpose is not to present detailed fish-growth experiments nor to defend Ecophys.Fish as some ultimate truth or even as the complete model of fish growth—although we are confident it can represent weight changes for fish in time-varying, multivariate environments better than any alternative model. That being said, we feel no particular obligation to justify our choices of functions and parameters, although we will try to explain those that are neither arbitrary nor obvious. In the model's assembly, we generally relied not on explicit empirical information (which we found woefully deficient), but rather on a combination of logic, generalized relationships from the literature, convenience, and trial-and-error. Always, we tried to be faithful both to the available data and to our joint understanding of the biological processes involved.

What we have in Ecophys.Fish is a complex set of intertwined hypotheses. Because the hypotheses are so interdependent, it will prove very difficult to test them critically, individually, or even as small subsets. This is not to argue that carefully focused experiments should not yield valuable improvements in the model's structure and parameters. But it is

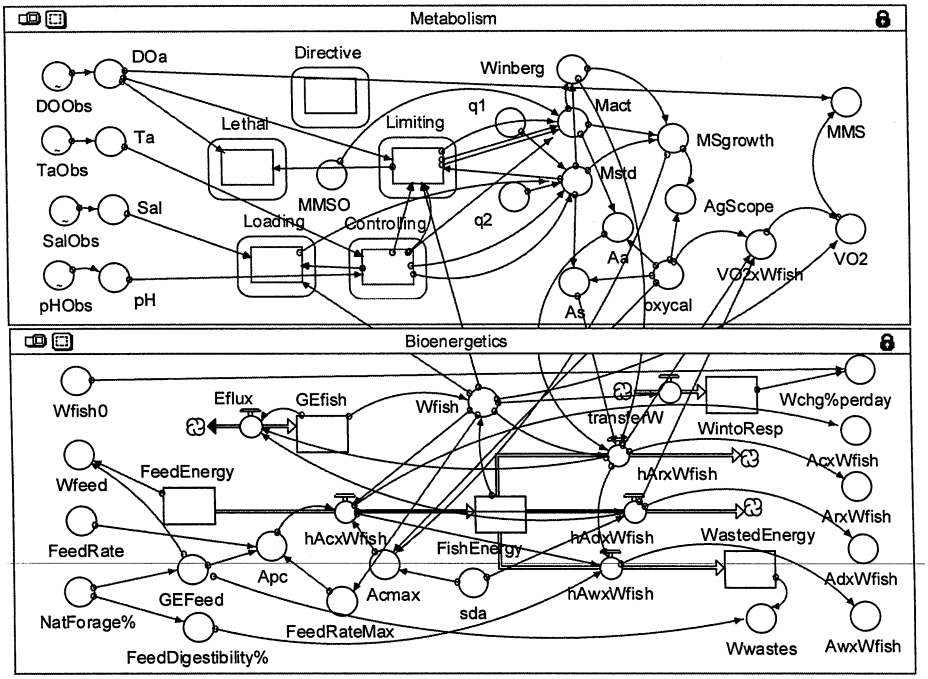

Figure 1. Ecophys.Fish: STELLA model of fish growth in response to ecophysiological factors.

to assert that the most efficacious and efficient way to move beyond the present version of Ecophys.Fish, will be to engage scientists with diverse interests and training, in thoughtful probing of the model's failings when it is tested with complex datasets from fish performance trials. One real advantage of Ecophys.Fish is that it explicitly accommodates joint temporal variation in physicochemical factors so that tests of Ecophys.Fish can be taken out of the controlled environment of the laboratory and into nature. Perhaps more importantly, tests can be taken out of the future and into the past, where much relevant research already has been bought and paid for.

Which brings us to our real agenda: We want to present Ecophys.Fish in such a way that our colleagues are sufficiently intrigued that they will consider, explore, evaluate, improve, and apply it. If we can achieve that, Ecophys.Fish will evolve, in our collective machines and minds, to become a worthy stage in the development of fish performance models that must be at the core of future fisheries science. Our pledge to those who would participate in the effort, is to give freely of whatever help we can. We begin here, with an exposition of Ecophys.Fish. The complete STELLA 6.0 code for the generic model can be examined at http://neilllab2.tamu.edu/EcophysFish/STELLAcode.pdf. To reinforce that, and to further minimize chances of miscommunication, we will maintain at http://neilllab2.tamu.edu, and available for FTP-download to anyone who wants it, a working copy of each specific model referenced in the following text. In these archived models and, thus, available for inspection and exploration, not only are all the rule sets, in explicit form, but also all the environmental data used in the simulations. In addition, the model library includes various model pieces (e.g., DOlim.stm) designed to facilitate understanding of Ecophys.Fish's internal workings.

STELLA 6.0 models will run on that and subsequent versions of STELLA, including the current version, which is 8.0 (April 2004). The runtime version of STELLA 8.0 is available for purchase at http://www.hps-inc.com/, at a nominal cost for noncommercial use. This runtime version of STELLA is fully functional, except "Save" and "Save as" are disabled.

Table 1 provides an index to text location of the first or primary reference to each Ecophys.Fish variable and parameter mentioned in the body of this article. We offer this index in lieu of the conventional table giving definitions, dimensions, etc., because we want to encourage the consideration of variables and parameters only in the full context of the model.

Table 1

Index to text-location of the first or primary reference to each Ecophys.Fish parameter and variable mentioned in the body of this article.

Parameter/Variable	Page	Parameter/Variable	Page
A	241	Mstd	240
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Apc	245	pHfactor	242
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Ecophys.Fish: The Red Drum Version

Ecophysiology of Red Drum

The red drum (*Sciaenops ocellatus*) is a fish of the warm-temperate, western Atlantic. This euryhaline sciaenid ranges from Cape Hatteras, NC, through the Gulf of Mexico, and into the Caribbean Sea; particularly along the Gulf coast, the red drum, or "redfish," is highly valued as a sportfish and foodfish. Red drum are voracious feeders (on shrimp and fish in nature and pelleted feeds in captivity) and grow rapidly, achieving weights up to 1 kg in the first year; maximum sizes exceed 30 kg. In the Gulf, declining stocks of red drum during the 1970s led to a ban on commercial fishing, intensive stock-enhancement efforts in Texas, and development of an aquaculture industry.

Physiological responses of red drum to environmental factors and their interactions (Neill, 1990) are consistent with the patterns typical of fishes (Fry, 1947, 1971; Brett and Groves, 1979; Neill and Bryan, 1991). Optimal and lethal (ultimate incipient) temperatures of red drum are about 28°C and 4–34°C, respectively—all other factors being optimal. The limiting level of dissolved-oxygen concentration (DO) for growth increases with increasing temperature. Again, all else being optimal, limiting DO is about 5 ppm at temperatures near and above 28°C; limiting DO declines to about 2 ppm at 18°C. Thus, the optimal temperature for growth falls when DO or any other limiting factor is at work. Food also limits, at least in nature. (In intensive aquaculture, it is DO that normally limits.) Even a maximum daily ration—for early-juvenile red drum, a daily mass equivalent to about $0.18*\text{Wfish}^{-0.27}$ (Wfish being the weight of the individual fish)—consisting of naturally energy-dilute food (i.e., gross energy ~1,000 cal/g) may be limiting at high temperatures and high DOs. Circumstantial evidence from intensive aquaculture (contrary hematological findings by Brown (1992), notwithstanding) suggests that pH < ~6.5 induces a substantial Bohr shift in red-drum hemoglobin's oxygen affinity, thus exacerbating negative metabolic impacts of low DO and high temperature. For the euryhaline red drum, tolerable salinities range from <1 ppt to > 60 ppt; optimal salinity seems to be near 10 ppt, which is just above the blood iso-osmotic point (Crocker et al., 1983; Forsberg and Neill, 1997). Based on natural history, there is an expected (but thus far undemonstrated) increase in the optimal salinity with size/age. Red drum, being very adept osmoregulators, exhibit only a 20–30% decline in growth performance as salinity diverges from the optimum to extremes of 1 and 45 ppt. However, there is a dramatic interaction between low salinity and low temperature: At levels of total dissolved solids approaching those of hard freshwater, ultimate lower lethal temperatures of juvenile red drum markedly increase, to values perhaps as high as 16°C (Procarione, 1986). This implies that metabolic costs of ion-osmoregulation (the added metabolic work imposed by salinity as a loading factor; Bryan et al., 1988) are greatly exacerbated by low temperature.

The information summarized in the preceding paragraph, organized with the insights deriving from the fish autecology and bioenergetics literature, provided the starting point for building an ecophysiological model of red drum growth.

Ecophys.Fish Overview

The model has two functional modules, metabolism and bioenergetics (Figure 1). The metabolism module has a STELLA space compression object (SCO) for each of the five classes of environmental factors. At present, the directive-factor SCO is entirely empty. The lethal-factor SCO accommodates the lethal effects of exposure only to low DO; however,

the other factors of environment are also involved, if only indirectly, via their effects on DO acclimation whose dynamics are linked with standard metabolism. In the loading-factor SCO, the salinity subroutine computes and returns a standard-metabolism intercept, which is multiplied by a function returned by the temperature subroutine in the controlling-factor SCO, and by $Wfish^{-0.20}$, to give standard metabolic rate. The temperature effect on standard metabolism is modeled as the product of steady state and transient state components, reflecting both the Ahrennius effect and thermal acclimation. The temperature and pH subroutines in the controlling-factor SCO both produce outputs that control active metabolism. These controlling effects are modeled as interactions with the limiting effect of DO in the limiting-factor SCO. Active metabolic rate also is modeled as weight-dependent, being proportional to $Wfish^{-0.22}$. At the core of active metabolic rate is the rate coefficient MMSO (Marginal Metabolic Scope Origin). We interpret MMSO to represent inherent metabolic efficiency of the fish-environment system after the effects of temperature, pH, DO, salinity, and fish size have been taken into account. Conceptually, the model parameter MMSO is the residual intercept of marginal metabolic scope, MMS (Neill and Bryan, 1991). Marginal metabolic scope offers a practical empirical measure of "water quality" from the fish's perspective and is relatively easy to determine, via routine respirometry (Neill and Bryan, 1991). Because many readers may be unfamiliar with MMS, its mathematical derivation is repeated at http://neilllab2.tamu.edu/EcophysFish/MMSderivation.pdf.

The present version of the model explicitly accommodates temporal change in environmental temperature and DO, by invoking physiological acclimation in the form of modified (variable rate coefficient) exponential lags in metabolic response. The rate coefficient for thermal acclimation varies from about 0.5/day at 18°C, to about 2./day at 34°C (Brett, 1946; Allen and Strawn, 1969; Hagar, 1978). The rate coefficient for DO acclimation is keyed to standard metabolic rate and ranges typically from 0.1/day to 0.5/day.

The bioenergetics module reflects conventional "rules of thumb" (Warren and Davis, 1967; Kitchell et al., 1974; Brett and Groves, 1979), with the addition of a component for metabolic limitation of food intake as suggested by the work of Jobling (1985) and recently embraced by van Dam and Pauly (1995). In keeping with Fry's thesis (Fry, 1947; 1971)—but contrary to the presumption of other fish-growth models (e.g., Kitchell et al., 1974)—physicochemical environment acts on the bioenergetics of Ecophys.Fish only through metabolism. Our model accommodates metabolic limitation of food intake by setting feeding rate to the minimum of (rate of food encounter, maximum rate of feeding and feed-processing, and metabolic scope for growth/sda). Consumed energy is converted to new fish biomass as a residual, after expenditures for standard and routine activity components of metabolism, feed-processing costs (about 15% of feed energy for natural feeds), and wastes (10–25% of feed energy for natural feeds). Our modeled fish conserves body form during times of feed limitation, by reducing caloric density of its tissues (within the range, 800 to the lesser of 1,400 or gross energy of feed, for red drum).

The model's inputs are time-series of temperature, pH, DO, salinity, food availability and energy content, and initial size and energy density of fish. Outputs are food consumption, standard and active metabolism, oxygen consumption, waste production, energy density of fish biomass, growth, and rate of low-DO mortality. Indirectly, the output is a measure of relative fitness of the fish-environment system to support fish growth.

Lethal Effect of (Low) DO

We do not consider Ecophys.Fish, in its present form, to properly represent the lethal effects of environment (thus the absence of "and mortality" in the title of this article). In particular,

the critical role of lethal temperature is not presently accommodated. But because the lethal effects submodel is relatively simple, and because, in keeping with Fry's view (Fry, 1947, 1971), we model mortality and growth as independent processes right up to the point of death, it is expedient to dispense with the lethal factor submodel, first-off.

There was no intent at the outset of Ecophys.Fish's development, to incorporate lethal effects. But, then, our very first field trial came with high mortality rates that seemed DO-related. And, so, we developed a simple dose-model that seemed to fit the data.

First, we decided that the fish might have accumulated a lethal dose of exposure to low DO as a function of some difference, DOstress, between ambient DO and DO acclimation state, DOaccl (see below, for more on DOaccl),

$$\text{DOstress} = \text{DOa} - \text{DOaccl}.$$

DOstress was then converted into an irreversible mortality dose, MORT, at the rate

$$\text{MORTinc} = \text{IF}(\text{DOstress} < -2.45)\ \text{THEN}\ -0.023^{*}\text{DOstress}$$

$$\text{ELSE}\ 0,$$

where the DOstress threshold, −2.45 mgO2/L, and the per-hour, per-unit DOstress rate of MORT incrementation, −0.023, were fitted to the mortality data from the FT01 field trial described below. The interpretation of the rule is that, whenever DOa is more that 2.45 mgO2/L below DOaccl, an irreversible mortality dose accumulates at the rate 0.023*DOstress, per hour. Thus, exposure of 4.0-mgO2/L-acclimated fish to 1.5 mgO2/L for 3 h should result in MORT = −0.023*−2.5*3 = 0.173/fish mortality, or the deaths of 17.3% of the individuals in the sample of fish.

Note that other components of environment have no direct impact on the lethal effect of low DO. They do, however, affect the process of DO acclimation, through their joint effects on standard metabolic rate. There is no converse effect of lethal low-DO dose on metabolism or growth. Under the model, survivors continue to perform metabolically at rates independent of their group's mortality rate.

Loading Effect of Salinity

Salinity, Sal, operates as a loading or masking factor. Because loading factors alter standard metabolism (Mstd; mgO2/(g*h)), it is convenient to have salinity, together with fish weight (Wfish; g), establish the base for Mstd, which is the intercept value S:

$$\text{S} = \text{Smin} + \text{Sgain}^{*}\text{Svar},$$

where, for red drum,

$$\text{Smin} = \text{Smino}^{*}\text{Wfish}\hat{}-0.2 = 0.1\text{mgO2}/(\text{g} * \text{h}) * \text{Wfish}\hat{}-0.2$$

is the minimum of S and occurs at the optimal value of salinity, SalOpt = 10 ppt. Away from SalOpt, S is elevated as a quadratic function of the difference between SalOpt and Sal, scaled by the difference between SalOpt and the relevant unit-loading value of salinity, SalL; the function is called Svar:

$$\text{Svar} = ((\text{Sal} - \text{SalOpt})/(\text{SalL} - \text{SalOpt}))\hat{}2,$$

where

$$\text{SalL} = \text{If}(\text{Sal} < \text{SalOpt})\ \text{Then}\ \ \text{SalLL}\ \ \text{Else}\ \ \text{SalUL},$$

and SalLL = 0.1 ppt and SalUL = 50 ppt are, respectively, the lower and upper unit loading values of Sal for juvenile red drum. The coefficient Sgain is a scaling parameter, and in keeping with the observations reported above, is presumed to be temperature-sensitive, increasing with cold stress (and decreasing with relief from cold stress) in red drum acclimated to temperatures below 18°C:

$$\text{Sgain} = \text{If (Taccl} > 18) \text{ Then } 0.003 \text{ (mgO2/(g} * \text{h))}$$

$$\text{Else } 0.003 + (0.0001 * ((18 - \text{Taccl})\text{^}2) * -\text{Tstress}),$$

where Taccl is the temperature (°C) to which the fish is acclimated (see below) and Tstress is the difference, Ta − Taccl. Note that, for red drum acclimated to temperatures above 18°C, these relations imply an increase in Mstd, over the Sal interval of SalOpt to SalL, of only about 3% for a 1-g fish, but more than 7.5% over the same interval for a 100-g fish. For the same two fish, but acclimated to 16°C and subjected to an ambient temperature of 10°C, Mstd is inflated at SalL by 5.4% in the smaller fish, and by 13.6% in the larger. Although these magnitudes of the salinity "load" may seem modest, their cumulative impacts on fish growth over time are large.

Shape of salinity's masking effect for red drum is generally consistent with Wakeman and Wohlschlag's (1983) experimental results. However, their data suggested a salinity load on metabolism two to three times larger than that invoked by our model. Model parameters were fit by trial-and-error, using results of a growth trial performed by co-author Craig on juvenile red drum (described below, p. 247).

Limiting Effect of DO

The effects of dissolved oxygen concentration (DO; mgO2/L = ppm) in the fish's immediate ambient environment (DOa) are modeled as a limiting effect on active metabolic rate (Mact; mgO2/(g*h)).

The limiting effect of DO on active metabolism is implemented with due regard for controlling effects of temperature and pH. DOlim is the temperature-dependent DO below which active metabolic rate becomes DO-dependent. The Hill equation, with an intercept of 0.35 mgO2/L and the Hill parameter set to 2.0 in the case of red drum, is used as the functional basis for computing DOlim:

$$\text{DOlim} = 0.35 + (\text{Tratio}\text{^}\text{Hill}/(1 + \text{Tratio}\text{^}\text{Hill})) * (1 - 0.005 * \text{Tstress}\text{^}2) * 8.15.$$

(The Hill equation will be familiar to blood physiologists as the power-hyperbolic relationship used to describe hemoglobin-oxygen association as a function of oxygen partial pressure; for a good summary treatment, see Cameron (1989).) Tratio is the ratio of ambient temperature, Ta, to inflection temperature, Tinfl—32°C for red drum; Tstress is the deviation of acclimation temperature, Taccl, from ambient temperature, Ta. For Tstress = 0 (fish acclimated to ambient temperature), fitted DOlim in red drum is 4.425 ppm at Ta = Tinfl, and increases toward 8.5 ppm as Tratio goes to infinity; as Tstress increases, DOlim diminishes (see DOlim.stm).

The adjusted DO (A; mgO2/L) for computing active metabolic rate is a fish-weight-adjusted minimum of DOa and DOlim, with the latter diminished by the Bohr effect when ambient pH < 7 (see pHfactor.stm, and A.stm):

$$\text{A} = \text{MIN(DOa, DOlim/pHfactor)} * \text{Weffect}.$$

Weffect is the proportion of A achieved by a fish weighing Wfish g, relative to that achieved by a 1-g fish:

$$\text{Weffect} = \text{Wfish}\hat{}\text{Wexp},$$

where for red drum, Wexp is −0.22.

DO-related responses are subject to physiological acclimation, over the interval ((0.45 ∗ DOlim = minDOaccl), DOlim). DOaccl varies over this interval as a negative exponential process, "decaying" toward DOa or the appropriate interval boundary, with rate coefficient raccl = Mstd (scalar)/day. This arrangement makes DO acclimation rate proportional to the rate of standard metabolism.

These relationships were based on the patterns typically observed for fishes (Neill and Bryan, 1991), and the parameter estimates were derived by trial-and-error, in fitting the model to data from growth experiments performed by co-authors Hutchins and Stahl (described below, p. 248).

Controlling Effects of Temperature and pH

Ambient temperature, Ta, has controlling effects on metabolism. Ta enters active metabolism via its contributions to Tratio and Tstress in the Hill equation (see previous section). In effect, the higher the value of Ta, the more the fish's metabolic capacity (the higher DOlim), provided the fish is acclimated to Ta (i.e., Tstress = Ta − Taccl = 0). Taccl exponentially decays toward Ta ≤ 34°C (for red drum) at a rate based on thermal acclimation experiments performed by Hagar (1978) on bluegill:

$$\text{kaccl} = \text{IF ((Ta} > 34\text{) AND (Taccl} > 34\text{)) THEN } 0$$

$$\text{ELSE } (24 * \text{EXP}(-2.15 + (\text{Taccl} - \text{Ta})/\text{Topt} - (((\text{Topt} - \text{Ta})/8.5)\hat{}2))),$$

where Topt for red drum is set to 28°C and kaccl has dimensions 1/h.

Ta controls standard metabolism, by exerting its well-known Ahrennius effect:

$$\text{Mstd} = \text{S}^{*}\text{EXP(q1}^{*}\text{Taccl)}^{*}\text{EXP(q2}^{*}\text{Tstress)},$$

where the intercept value S is elevated as an exponential function both of acclimation temperature (Taccl, the steady state component) and of the difference between ambient and acclimation temperatures (Tstress, the transient state component). The steady state rate constant q1 was set to 0.05/°C (equivalent to $Q_{10} = 1.65$), based on results of experiments conducted by co-author Hutchins (unpublished; also, see below, p. 248). The transient-state rate constant q2 was set arbitrarily to 0.09/°C ($Q_{10} = 3.0$), thus assuring a modeled fish in which standard metabolism partially compensates for temperature change.

Ta also controls active metabolism, Mact, by affecting the capacity of the respiratory and circulatory systems to supply oxygen to the fish's tissues. Mact's central component, DOlim, already has been presented; it is this power-hyperbolic function that gives Mact vs. Ta its characteristic sigmoid shape. (For red drum, however, the fitted parameters of DOlim, and, thus, of Mact, are such that the curve inflects near the high end of the thermal spectrum, rendering the $\int$-shape without most of its upper half. See DOlim.stm and Mact.stm).

Under Ecophys.Fish,

$$\text{Mact} = \text{MMSO}^{*}\text{pHfactor} * \text{A} * \text{DOlim} * \text{DOaccl}\hat{} - 0.9,$$

where MMSO (L/(g*h)) is the intercept of marginal metabolic scope; A, DOlim, and DOaccl are as defined above; and pHfactor is a dimensionless transform of pH designed to enable

implementation of a crude Bohr effect. pHfactor is 1. for values of pH above 7.0, then decays exponentially, with rate constant pHgain, as pH deceases below 7.0:

$$\text{pHfactor} = 1 - \text{EXP}((-\text{pHgain}/\max(0.01, (\max(\text{pH}, 7) - \text{pH})))),$$

where for red drum, pHgain is set to 0.56. Thus, pHfactor is 0.674 at pH = 6.5, 0.429 at pH = 6, and 0.244 at pH = 5.

Interpretation of Mact's functional relations is facilitated by dichotomizing Mact within its component function A, the effective DO:

If DOa < DOlim/pHfactor

$$\text{Then Mact} = \text{MMSO}^*\text{DOa}^*\text{pHfactor}^*\text{DOlim}^*\text{DOaccl}^\wedge - 0.9^*\text{Weffect}$$

$$\text{Else Mact} = \text{MMSO}^* \qquad \text{DOaccl}^\wedge - 0.9^*\text{Weffect}.$$

Thus, for values of DO that are limiting given pH, Mact is directly proportional to ambient DO, with a slope that is the product MMSO*pHfactor*DOlim*DOaccl^ −0.9*Weffect—i.e., a slope that increases with MMSO, pH (given that pH < 7), and DOlim (i.e., Ta), and decreases with DOaccl (almost as its linear inverse) and fish weight. For values of DO above that limiting given pH, Mact is independent of DO, but is directly proportional to MMSO and inversely proportional both to DOaccl and fish weight. Mact.stm is offered, to help in visualizing and exploring these relationships.

The reader will have observed, by this point, that the effects of salinity, DO, pH, and temperature are intertwined to the degree that it is impractical, if not impossible, to separate the whole of their integrated effects into component parts, even for sake of presentation.

Metabolic Scope, Metabolic Scope for Growth, MMS, and the Winberg Factor

Fry (1947, 1971) defined the metabolic scope for activity (MS) as the difference between active and standard metabolic rates, Mact − Mstd. Neill and Bryan (1991) emphasized the utility of a MS subset that they called the metabolic scope for growth (MSgrowth) and defined as the difference between active and routine metabolic rates, Mact − Mrtn. Mrtn varies between Mstd and Mact, depending on the impact of directive factors. After a fish has spent several hours in the solitude and quiet of a darkened respirometer chamber, the fish's Mrtn can approach its Mstd; in nature (and just after undergoing the trauma of insertion into the respirometer chamber), the fish has a Mrtn that can approach its Mact. One advantage of MMS as a measure of capacity for metabolic performance is that its components, the routine rate of oxygen uptake (VO2r, presumed to be one-to-one with Mrtn, the routine rate of oxygen demand) and the limiting DO for that rate (LOCr), tend to compensate for variation in one another so that their ratio MMS = VO2r/LOCr remains stable despite variation in Mrtn and, thus, in VO2r. However, when one proceeds to the next step, and tries to use MMS to estimate MSgrowth, by applying the relation (Neill and Bryan, 1991)

$$\text{MSgrowth} \sim \text{MMS}^*\text{DO} - \text{VO2r},$$

the actual magnitude of VO2r must come into play. Although Ecophys.Fish uses a more sophisticated approach in estimating MSgrowth, the same issue—activity-induced variation in the magnitude of VO2r—must be managed. Because in nature (and even in the respirometer chamber), the level of nongrowth activities (including loads induced by locomotion, disease- and parasitism-related stress, and excitement/anxiety) is difficult or impossible to know, the inflation of Mrtn by loading and directive factors is represented by the application of a "Winberg" factor. Winberg (1960) deduced that the routine metabolism of fish in nature

is about twice that in respirometer chambers. This idea has found indirect support in the theoretical work of Weihs (1973), and it has been embraced by students of fish bioenergetics (Ware, 1975; Kitchell et al., 1978). We adopted it in Ecophys.Fish, for lack of any practical alternative.

A note on terminology: Winberg (1960) used routine metabolic rate (Mrtn) to mean that consistent with VO2 in a fasting, routinely active fish after several hours habituation in a darkened respirometer chamber shielded from extraneous stimuli. Our view is that Mrtn under such conditions approaches Mstd. For this reason, we adopted the position in parameterizing Ecophys.Fish, that Mstd's intercept could be estimated as one-half the routine metabolism determined by trial-and-error simulation of growth trials. Thus, one might consider our "Mstd" a respirometry Mrtn that then should be doubled to estimate Mrtn of fish under aquacultural or natural conditions. As it turned out, we were able to use respirometry, in conjunction with the model, to estimate the actual magnitude of the Winberg factor (see below, p. 262).

Metabolic Scope for Growth and Maximum Feeding Rate

One virtue of MSgrowth is that it can be linked to maximum feeding rate, via Winberg's (1960) empiricism. Under Ecophys.Fish,

$$\text{MSgrowth} = \text{Mact} - \text{Winberg}^{*}\text{Mstd},$$

where Winberg is nominally 2.0. Because, logically,

$$\text{VO2max} = \text{Mact} = (\text{Mrtn} + \text{Msda})\text{max}$$

—i.e., the maximum rate of oxygen uptake equals the maximum rate of oxygen use, which, in turn, corresponds with maximum rates of routine and feed-processing metabolism, Msda—and because

$$\text{Msda} = \text{sda}^{*}\text{Ac}/\text{oxycal},$$

where Ac is feeding rate (energy/(Wfish*t)), oxycal is the oxycaloric equivalent (3.4 cal/mgO2—Brett and Groves, 1979) and sda is the proportion of the feed's energy used in processing the feed (including, but not limited to, "specific dynamic action"), typically about 0.15 for natural forage (Warren and Davis, 1967), we presumed that

$$\begin{aligned}\text{VO2max} = \text{Mact} &= \text{Mrtn} + \text{sda}^{*}\text{Acmax}/\text{oxycal} \\ &= \text{Winberg}^{*}\text{Mstd} + \text{sda}^{*}\text{Acmax}/\text{oxycal};\end{aligned}$$

therefore,

$$\text{Acmax} = (\text{MSgrowth}/\text{sda})^{*}\text{oxycal}.$$

In effect, this relation implies that a fish's maximum feeding rate ought to be in balance (via evolution) with its metabolic scope for growth, with due consideration of the fact that only the feed-processing "overhead" need be paid from current metabolism; if sda = 0.15, this means that Ac can be up to 1/0.15 = 6.67 times the magnitude of MSgrowth, when the two are converted to common dimensions via an oxycaloric equivalent.

Of course, limited availability of feed, or limited capacity of the fish to eat and digest available feed, may set a prior limit on feeding rate. These relations are accommodated under Ecophys.Fish by setting the energy-input rate to

MIN(Apc = MIN(FeedRate, FeedRateMax)*GEfeed/24 = hourly rate at which feed energy is presented (to the metabolic subsystem) for processing,

Acmax = (MSgrowth/sda)*oxycal = metabolism available to support feed processing and assimilation).

The components of Apc are as follows:

FeedRate = daily rate of feed presentation = daily feed encounter rate,

FeedRateMax = 0.18*Wfish^(0.0105*LOGN(Wfish) − 0.25)

= maximum daily rate at which feed can be consumed and physiologically processed, and

GEfeed is gross energy content (cal/g) of the feed as consumed.

All these determinants of feeding rate are converted into the hourly, per-fish rate of feed-energy consumption, hAcxWfish, by multiplying the appropriate daily, per-gram rate by Wfish g and dividing by 24 h/day.

FeedRateMax is the maximum daily rate of feed consumption under metabolism- and feed-unlimited conditions. FeedRateMax is apparently equivalent to the "maximum daily ration" of Kitchell et al. (1974, 1978) and many others. We began with the usual assumption of a simple power function to describe the effect of fish weight on FeedRateMax, but inability to fit growth-trial data over a range of red drum weights obligated us to adopt the more complex function presented above. In effect, our FeedRateMax model invokes an increasing power of weight as the fish get larger— −0.250 at 1 g, −0.226 at 10 g, −0.202 at 100 g, and −0.178 at 1 kg. The intercept value of FeedRateMax, for Wfish = 1 g, is 0.18 gfeed/(gfish*day), or 18% of body weight per day. (An interesting implication of this trend in the Wfish-power of FeedRateMax, is that there may exist for red drum a bioenergetic "bottle-neck" at a value of Wfish near 100 g, if GEfeed is limiting.)

Because FeedRateMax is mass-based, fish eating energy-rich prepared feeds, with GEfeed typically 4,000 cal/g or more, are much more likely to be metabolism-limited than are fish eating natural feeds that typically contain only about 1,000 cal/g. This is especially true at low temperature, because MSgrowth tends to decline with temperature.

Conversion of Feed (and Oxygen) to Flesh: Growth and Bioenergetics

Under Ecophys.Fish, FeedEnergy passes at the rate hAcxWfish to an energy pool, FishEnergy, which is partitioned hourly as expenditures related to routine metabolism (hArxWfish), feed-processing metabolism (hAdxWfish), and eliminated wastes (hAwxWfish). Residual FishEnergy is stored as new fish biomass, thus incrementing Wfish. Note that the "currency" for all bioenergetic transactions is energy, despite the fact that it is mass that modeled fish consume as feed and grow (or don't grow) as new tissue.

The three expenditure terms, hAixWfish, are consistent with those met with in most fish-bioenergetics models. hArxWfish is the hourly, per-individual cost of routine metabolism = Winberg*Mstd*oxycal*Wfish, not to exceed Mact*oxycal*Wfish. hAdxWfish is the corresponding cost of feed-processing, sda*hAcxWfish. The hourly, per-fish rate of energy loss

as wastes is

$$\text{hAwxWfish} = ((100 - \text{FeedDigestibility\%})/100)^{*}\text{hAcxWfish} + 0.05^{*}\ \text{MAX}(\text{hAcxWfish},\ \text{hArxWfish}).$$

The first term is for fecal loss and the second is for nitrogenous excreta. The implied argument is that the nondigestible (nonassimilable) parts of the ration—typically, 10–25% for natural forages—are passed as feces, and that nitrogenous wastes amount to 5% of the ration or routine metabolism, whichever is most.

Satisfactory fits of the model for red drum weight change over extended periods of time seemed to demand that GEfish, the energy-density of fish biomass, be allowed to change with the rate of feeding relative to the rate of metabolism. This sort of feeding-related flux in energy density is regularly observed in fishes (Kitchell et al., 1977a) and would seem to reflect an adaptive response involving the conservation of body form for hydrodynamic reasons, over a range of nutritional planes: during times when feed is abundant, lipid replaces water and GEfish rises; when times are lean, water replaces lipid and GEfish declines. Based on our experiences with red drum, we decided to let GEfish range between 800 and 1400 cal/g, but not to exceed GEfeed. The (rather arbitrary) rule adopted was

IF (hAdxWfish $<$ 0.2*hArxWfish) AND (GEfish $>$ 800)

THEN ($-$(0.003/24)*GEfish)

ELSE (IF (hAdxWfish $>$ 0.2*hArxWfish) AND (GEfish $<$ 1400)

THEN ($+$(0.003/24) $*$ GEfish)

ELSE 0).

Thus, if the fish is nutritively stressed (feed-processing metabolism less than 0.2 of routine metabolism) and still has an energy density higher than the allowable minimum, then energy density is reduced at 0.3%/day; otherwise, provided the fish's energy density has not exceeded the 1,400 cal/g allowable maximum, energy-density increases at 0.3%/day. This rule has the effect of damping extreme fluctuations in Wfish that otherwise would occur when environmental conditions fluctuate between those promoting and restricting feeding.

Ecophys.Fish Parameterization Trials for Red Drum

Four growth trials in the laboratory and one in ponds were the basis for refining and parameterizing Ecophys. Fish for red drum. The pond trial is described in Garces' (1991) doctoral dissertation, but none of the four lab trials has been published, even in thesis form. However, the primary investigator of each lab trial is a co-author of this article, and each of the trials is described here in sufficient detail to permit the reader to understand the parameterization context.

All four laboratory growth trials involved similar methods and materials. Juvenile red drum, produced from captive parents in Texas hatcheries, were tested in 100-L glass aquaria, each with its own biofilter or connected with other aquaria in a recirculating system containing a common biofilter. In the three trials conducted at Texas A&M's Aquacultural Research and Teaching Facility, near College Station, TX, the culture medium was synthetic seawater (Fritz Aquaculture), but diluted or concentrated to achieve the nominal salinity at which the trial was performed; in Stahl's DO experiment, conducted at Texas A&M University-Corpus Christi, Corpus Christi, TX, the medium was diluted natural seawater from the Port Aransas, TX, ship channel. In all experiments, the medium lost to evaporation and

in siphoning wastes was replaced at a rate of 5–10% per day. The fish were fed pelleted feed twice daily at a rate intended to ensure satiation; gross energy and digestibility of the feed, especially formulated for red drum (Moon and Gatlin, 1994), were about 4,000 cal/g (as fed) and 85%, respectively. Fluorescent lighting, from fixtures above the aquaria, was switched by timers to provide a 14-h-light, 10-h-dark photo period. Values of pH were 7–8.5 (except when low-pH treatments were imposed—see below). Temperature was managed via thermostatic control of ambient air temperature in the laboratory, except that in Hutchins' temperature experiments, temperature of individual aquaria was controlled (within about 0.3°C) via electrical immersion heaters switched by mercury-contact thermoregulators, acting in opposition to chilled ambient air in the laboratory. Except in Stahl's DO experiment (see below), individual aquaria were supplied with compressed air, supplemented as necessary with compressed oxygen, to ensure DOs near air saturation. Environmental variables were measured at least twice daily and adjusted to nominal values as necessary. Experimental treatments were imposed on duplicate or triplicate groups of 10–40 fish per aquarium, with the replicate aquaria arranged to achieve a randomized, complete block design. The group of fish in each aquarium was counted and weighed, en-mass, at the trial's beginning, its end, and at weekly or bi-weekly intervals in between. Laboratory growth trials lasted 5 to 8 weeks, following a 1-week conditioning period.

Our strategy was to organize the laboratory trials in a sequence such that the environmental variables of primary interest—temperature, DO, and salinity—were tested in order of decreasing uncertainty about optimum values. Because we were confident from previous experience with red drum growth, that best performance would occur between 25 and 30°C and at DOs near air saturation, we focused first on salinity.

Craig performed the salinity trial, using red drum with an initial mean weight of 3.5 g. Salinities tested were 1, 5, 10, 15, 25, 35, and 45 ppt. Nominal temperature was 27°C, and supplemental oxygen was used to ensure DOs near air saturation. Experiment-wise growth rates, relative to those we had observed in other experiments, were high with mean weight-gain over this 56-day trial exceeding 1,000% at every salinity. Maximum growth rate occurred near 10 ppt. Ecophys.Fish gave an acceptable fit to the relationship between final fish weight and salinity, with MMSO set to 0.314 L/(g*h) (SalSteve.stm; Figure 2).

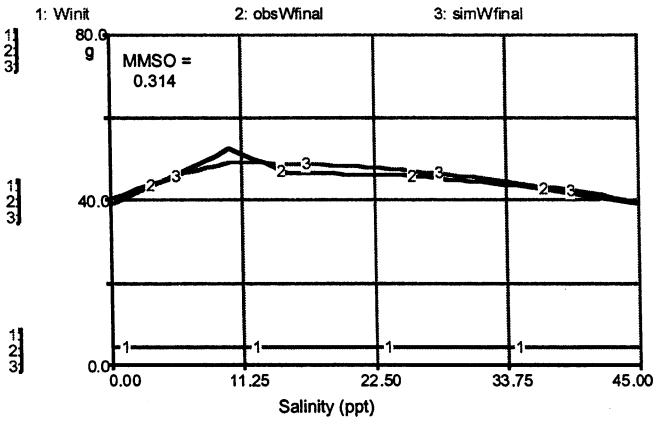

Figure 2. Red drum growth vs. salinity, SalSteve. Values of obsWfinal and simWfinal are final observed (mean) and simulated weights of red drum starting the growth trial at Winit.

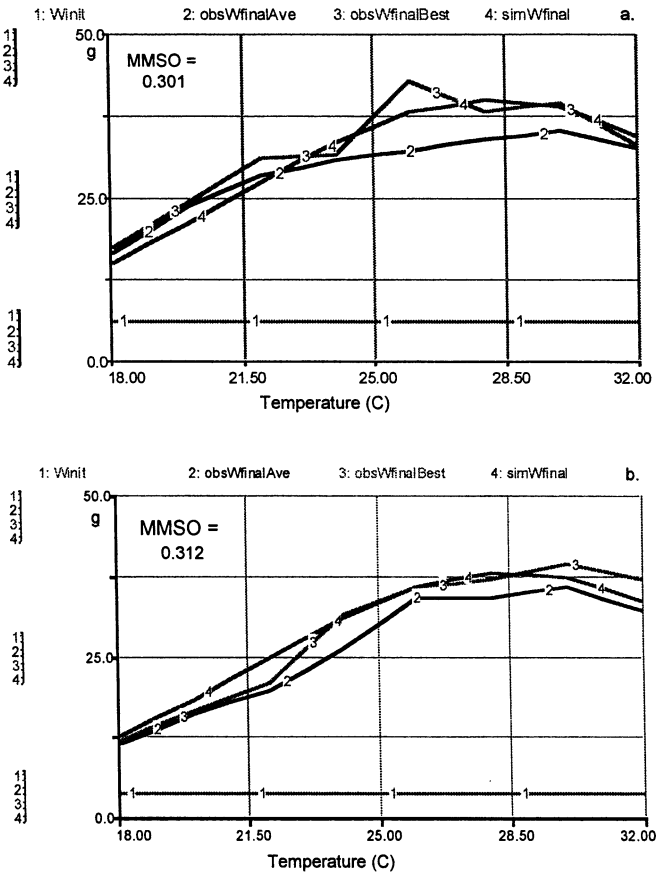

Figure 3. Red drum growth vs. temperature, Ta1Cynth (a) and Ta2Cynth (b). Values of obsWfinalAve and obsWfinalBest are the terminal mean weights of fish averaged over three replicate groups at each temperature, and the terminal mean weight of fish in the replicate group that ended the experiment with the greatest mean weight, respectively.

Next, Hutchins performed two temperature trials, each 49 days in duration. The first involved fish with an initial mean weight of 6 g; the second used fish with an initial mean weight of 3.6 g. In both experiments, salinity was maintained near 10 ppt, and DOs were kept near air saturation via a combination of compressed air and oxygen. Temperatures tested were from 18 to 34°C, at 2-°C intervals. The two trials gave similar results, in that maximum weight gain occurred near 28°C. Ecophys.Fish gave an acceptable fit to both sets of final weight vs. temperature data, with MMSO set to 0.301 in the first trial (Ta1Cynth.stm; Figure 3a) and 0.312 in the second (Ta2Cynth.stm; Figure 3b).

Toward the end of Hutchins' first temperature trial, we estimated routine VO2s of the fish en-mass, by performing a mass balance on DO (Oborny, 1993; Neill et al., 2004). In effect, we estimated oxygen uptake rate for the fish in the treatment aquaria as the difference between the estimated rates of oxygen resupply via aeration and removal via chemical and biological agents other than the fish. Results conformed to expectation, in that apparent VO2 increased exponentially with temperature; Q10 for the response was about 1.72. Moreover, the regression of VO2 on temperature fell within the interval (Mstd, Mact) estimated for 20-g fish under Ecophys.Fish (Ta1Cynth.stm; Figure 4).

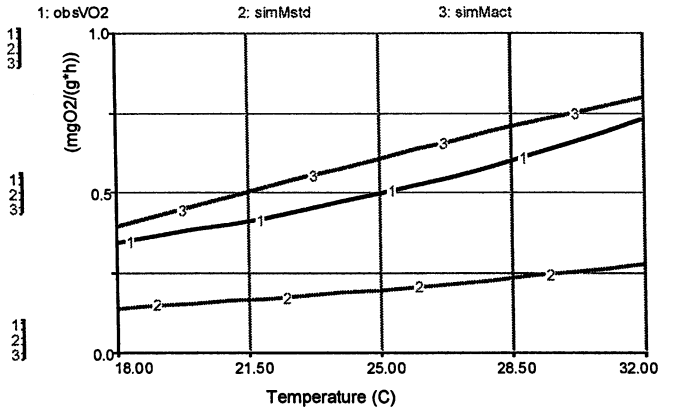

Figure 4. VO2 relative to Mact and Mstd in red drum vs. temperature, Ta1Cynth. Mact and Mstd are for simulated fish at 20 g (Ta1Cynth.stm), approximate weight of real red drum when VO2 was measured.

In Hutchins' second temperature trial, a test of low-pH effects was superimposed on the temperature treatment at 28°C. Although pH control was problematic and ultimately failed, the data from the early part of the trial suggested that reduction of pH from 7.5–8.5, to 6.0–6.5, caused growth rate to be reduced about 50%, under normoxic conditions.

Stahl performed two growth trials designed to measure effects of low DO on growth of juvenile red drum. Control and measurement problems spoiled the first trial; so, only the second was used in parameterization of Ecophys.Fish. Nominal temperature and salinity in this second trial were 27°C and 10 ppt, respectively. In the recirculating aquarium system where the trial was conducted, DO was managed by passing the water returning from the system's external biofilter through a three-stage "stripping column" where some of its dissolved oxygen was exchanged for nitrogen. The individual aquaria then received effluent tapped from the stripping column at points appropriate for maintaining their DOs at six nominal levels, ranging down to 30% of air saturation. Maintenance of low DOs was facilitated by tank "covers" of 3-mm-thick clear acrylic plastic that floated just beneath the water surface, thus occluding about 95% of the air-water interface. Initial weight of fish used in this 35-day growth trial was 2.5 g. The parameterized model, with MMSO optimized at 0.283, generated final fish weights in good agreement with observed results (DO2Chris; Figure 5). But because DO fluctuated over time within treatments, observed and simulated final weights could be graphed only against the DO treatment class, not the level of DO itself.

It was our original intent to conclude the parameterization effort with a multiple factor growth trial in the laboratory. But instead, we used an existing dataset from a field trial done some years earlier, in Panama, and described by Garces (1991). In that trial, red drum were cultured in nine ponds at the Mida Research Station over an 11-month period. The fish were sampled and weighed at bi-weekly intervals; daily records of environmental variables (early morning) and rates of feed application were maintained. Over the 336-day trial, the fish grew from an initial mean weight at stocking of 1.6 g, to 659 g at harvest, averaging over all nine ponds. Although temperature varied only modestly in the tropical system, DO declined with the increasing biomass of fish and oxygen-demanding waste load, and salinity varied from near 10 ppt during the wet season to about 40 ppt during the dry season. Ecophys.Fish, with MMSO optimized to 0.297, provided a very acceptable fit to the Mida fish weight vs. time data (MidaHumberto.stm; Figure 6). In fitting the Mida trial, the only

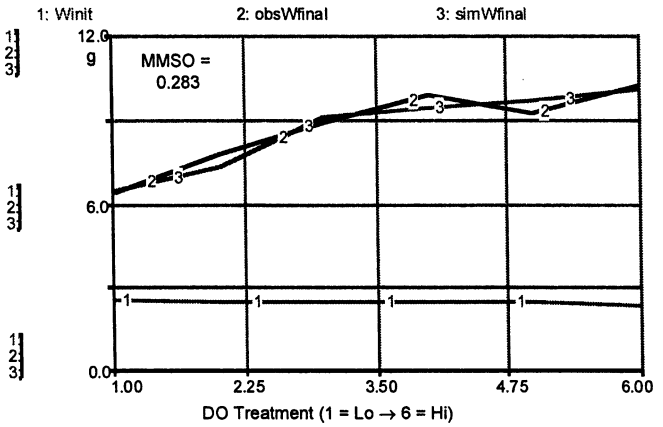

Figure 5. Red drum growth vs. DO-treatment, DO2Chris.

parameterization adjustments made to the model were in the range of allowable GEfish and in MaxFeedRate's fish weight dependencies.

Comparing rates of fish-weight change (Wchg) observed vs. simulated under Ecophys.Fish for all five parameterization trials indicated a very high degree of concordence (Figure 7). The linear-regression equation for the five datasets combined was

$$\text{obsWchg} = 0.071 + 1.002^{*}\text{simWchg (\%/day)},$$

with $R^2 = 0.986$ (n = 37). In this evaluation, the average replicate (salinity and DO trials) or fastest growing replicate (both temperature trials) value of per-fish average obsWchg was computed over the entire trial for each treatment and regressed on the corresponding value of simWchg, in the case of the four lab trials; but, in the case of the Mida pond trial, the value of obsWchg, averaged for the nine ponds, was computed over the eight consecutive 42-day intervals of the trial. Our thinking, with regards to the Mida trial, was that parameterization success would be better judged by goodness-of-fit averaged over ponds but assessed within time-intervals, than averaged over time-intervals (i.e., measured over the entire trial) but assessed within ponds. To assure that simulated Mida fish started each 42-day interval at

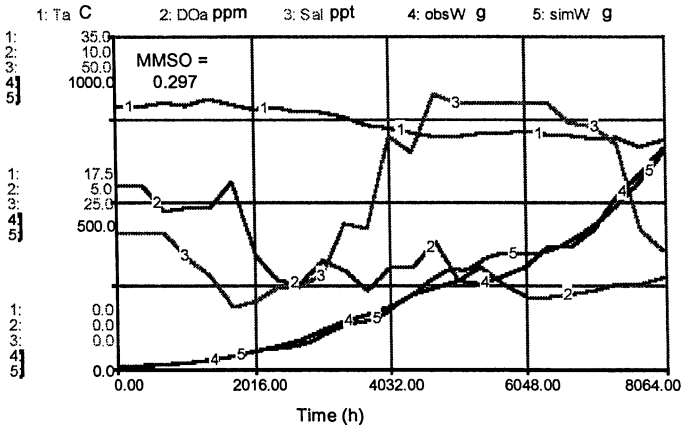

Figure 6. Mida grow-out trial, MidaHumberto.

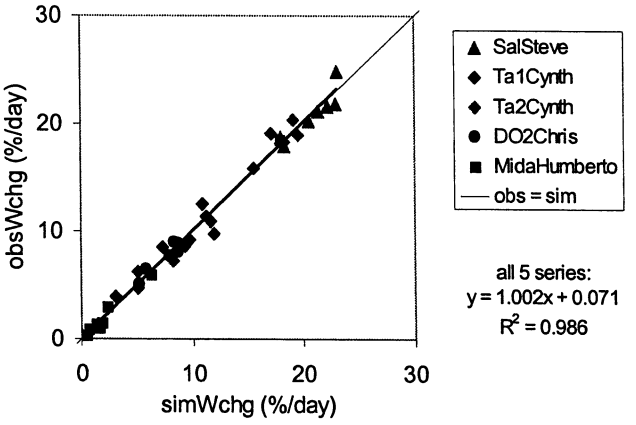

Figure 7. Observed vs. simulated rates of weight change, in five parameterization trials of the model for red drum.

the observed weight and with the same environmental history as the real fish, the simulation of performance over each interval was started at trial time-0, but with initial fish weight altered (by trial-and-error) from the actual value (1.6 g) to that necessary to give no error between fish weight simulated and observed at the beginning of the 42-day interval at issue. For example, to produce a simulated fish that began the last 42-day interval, on day 294, with the observed mean weight, 416 g, it was necessary to start the simulation with Wfish0 set to 1.28 g.

The purpose of these convolutions was to minimize the potential problem of statistical time-dependence among observations within the Mida trial, and to give approximately equal statistical weight to the five trials. Of the 37 points graphed in Figure 7, the contribution of values from the five trials ranged from 6 to 8. Although statistical significance is not at issue—this being not a test of the model, but a report on the success we had in parameterizing it—we thought it important to represent that success in a fair and conservative way.

Parameterization Experiments That Ecophys.Fish Would Not Fit

. . . And fairness demands, too, that we present the case of a pair of laboratory growth trials that Ecophys.Fish was reluctant to fit. Those growth vs. temperature experiments were done by Tomasso and Kempton (2000) at Clemson University, South Carolina, at about the same time Hutchins was doing similar experiments at Texas A&M.

Tomasso and Kempton's 56-day-long experiments were done in FrigidUnit^{TM} raceways. The juvenile red drum were fed pelleted feed at a rate of 8%/W per day. Levels of Ta were 18, 22, 26, 30, and 34°C. In the first experiment, mean initial fish weight was 32.3 g. Nominal salinity was 10 ppt, and average DOa was maintained above 6.2 mgO2/L in every temperature treatment. Ecophys.Fish, with MMSO optimized at 0.274, indicated a clear thermal optimum for growth, at 26°C (Ta1JoeNom.stm); whereas, the real fish achieved greatest final weights at about 30°C, with not much diminution at 34°C (Figure 8a). In the second experiment, mean initial fish weight was 21.6 g. Nominal salinity was 5 ppt, and average DOa was maintained above 5.4 mgO2/L in every temperature treatment. Both simulated and observed patterns of weight change were the same as before: Simulated weight

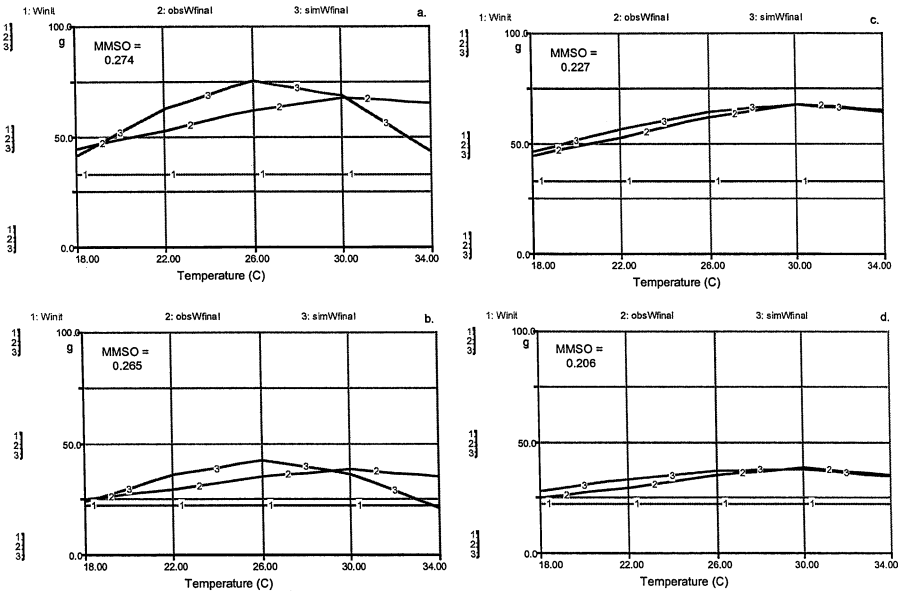

Figure 8. Red drum growth vs. temperature, (a) Ta1JoeNom, (b) Ta2JoeNom, (c) Ta1JoeAlt, and (d) Ta2JoeAlt. Under the nominal model, Winberg = 2; under the alternative model, Winberg = 1 + 0.5*(Mact – Mstd)/Mstd.

change (with MMSO optimized at 0.265) peaked at 26°C (Ta2JoeNom.stm), but observed weight change was greatest near 31°C, and almost as great at 34°C (Figure 8b).

We were unable to manipulate Ecophys.Fish's parameters for a better fit. However, we did find a functional change in the model itself that proved effective: Co-author Miller suggested we try a modification of the Winberg factor—that we suppose fish use a fixed fraction of their metabolic scope (MS) for routine activity (and that this fraction just happens to be equivalent to standard metabolic rate (Mstd), under environmental conditions that produce near-maximum MS—thus, Winberg's (1960) conclusion that Mrtn = 2*Mstd). So, we replaced Ecophys.Fish's standard Winberg function,

$$\text{Winberg} = 2 \text{ (nominally)},$$

with

$$\text{Winberg} = 1 + 0.5^{*}(\text{Mact} - \text{Mstd})/\text{Mstd}.$$

Under this alternate Winberg function, the fish uses half its MS for routine activity. Thus, at both thermal extremes, where MS goes to zero, there is no routine activity. Under the standard Winberg function, the allocation of MS for routine activity is an exponentially increasing function of temperature (being a fixed multiple of Mstd), and therefore, routine activity consumes all of MS at temperatures higher than that at which

$$\text{Winberg}^{*}\text{Mstd} = \text{Mact}.$$

The consequence is that MS for growth goes to zero at a lower temperature under the standard Winberg function than under the alternate function.

Ta1JoeAlt.stm and Ta2JoeAlt.stm, equipped with the alternate Winberg function (but otherwise identical to the standard version of Ecophys.Fish) and with MMSO optimized

to 0.227 and 0.206, respectively, gave very good fits to both of Tomasso and Kempton's experiments (Figures 8c and 8d). Moreover, we think the alternate Winberg function has considerable intuitive appeal. So why did we not adopt it, over the standard Winberg function? The answer is a bit involved: To begin, we could not get the alternate model to fit either of Hutchin's temperature trials. So, it then became a matter of choosing which trials to fit—Hutchins' or Tomasso and Kempton's. We opted to use the model variant that fit Hutchin's trials, because her fish exhibited much faster, and what we consider more normal, rates of growth than did Tomasso and Kempton's. Although the starting sizes of Hutchins' fish were much less than Tomasso and Kempton's, the difference in growth rates was too great to be ascribed to a weight effect. In fact, if only Hutchins' and Tomasso and Kempton's second experiments are compared, the fish of the fastest growing treatment ended their respective trials at about the same weight—38 g. But Hutchins' fish started their trial much smaller than Tomasso and Kempton's—3.6 vs. 21.6 g. Moreover, Hutchin's trial was only 7 weeks long, compared to the 8 weeks of Tomasso and Kempton's.

Even after considerable discussion, we have been unable to find a good explanation for the slow rates of growth in Tomasso and Kempton's fish. And we remain intrigued by the alternate Winberg function. But, at this point, we feel compelled to stay with the original.

Evaluation of Ecophys.Fish for Red Drum: Conceptual Consistency and Field Tests

The move to evaluate Ecophys.Fish as a tool for understanding the joint effects of environment began, of course, during the model's construction and parameterization phases. At each step, we not only tried to fit the model to the data generated by the parameterization trials, but also we did our collective best to make sure we started and stayed with a set of functional relationships that made good biological sense—or at least ones not in conflict with existing knowledge. As we proceeded with parameterization, we constantly discussed and explored the model's responses to various environmental scenarios. What we looked for were signs of conceptual consistency with published relationships; what we hoped for were insights about relationships yet unknown (or unheralded). Before proceeding to a description of field tests of the model, we will present one example of the model's conceptual consistency with expected patterns. (Ultimately, we will return to the "new insights" issue.)

If Ecophys.Fish worked as intended, it should be able to produce realistic patterns of growth in response to interacting temperature and DO. To find out, we simulated Hutchins' second temperature trial, but with DO set to constant values of 2, 3, 4, and 6.5 mg/L. As expected, growth was progressively limited by decreased DO, and the limitation was greatest at high temperatures (Ta2Cynth.stm; Figure 9). The result of the interaction between the limiting effects of low DO and the controlling effects of temperature was a reduction in the optimum temperature for growth with declining DO—from near 28°C at DOs near and above 6.5 mg/L (the nominal DO in Hutchins' trial), down to about 26°C at DO = 2 mg/L. The emergent relationship is very similar to the conventional representation of metabolic scope vs. the same variables (cf. Figure 3 in Neill and Bryan (1991)).

Vega was the primary investigator in empirical tests of Ecophys.Fish for red drum (Vega, 2003). He conducted a series of field trials with red drum caged in the Packery Channel (PC) area of Corpus Christi Bay; in ponds at the CCA/CP&L Marine Development Center (MDC) in Flour Bluff, TX; and, in the CP&L power plant cooling reservoir in Flour Bluff. All three locations are within 10 km of one another and lie on the southern edge of Corpus Christi, a Texas city on the Gulf of Mexico. In this part of the western Gulf, the diel amplitude of gravitational tides is less than 0.5 m, and coastal waters inside the barrier island system typically are hypersaline. Habitats presented to the caged fish ranged from plastic-lined

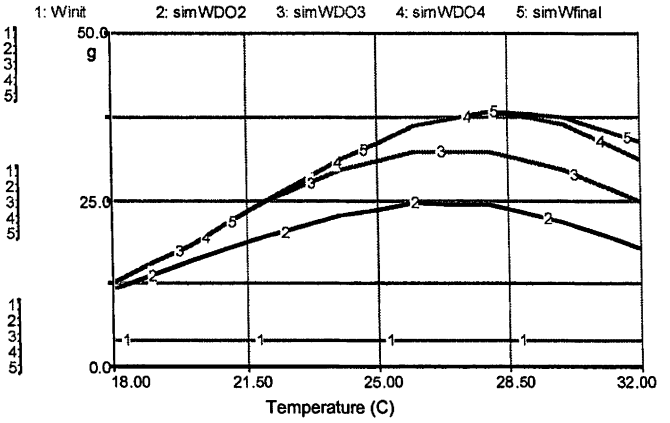

Figure 9. Interaction of limiting DO and temperature, Ta2Cynth.stm.

ponds (at MDC); to dredged and bulk-headed canals with mucky bottoms (PI site within the PC area); to open "flats" with mud, sand, and shell substrate, partly vegetated by *Halodule* and other seagrasses (the PC proper and the CP&L cooling reservoir). Reported on here is a subset of six trials from among the 15 Vega performed (the selected subset being those trials that had been fully analyzed at the time this article was originally drafted).

Our strategy was to use natural or quasi-natural differences in environment to generate contrasting growth rates, then test Ecophys.Fish's ability to account for the observed variation in growth rate. By confining the fish to cages (in some trials, other fish were released at the cage site), we hoped to minimize the role of directive factors and to exclude predation as a lethal factor. We wanted to determine how well the model could process information on physicochemical environment (monitored either with hand-held instruments on a two- or three-time-per-day basis, or with YSI 6000 dataloggers deployed continuously at the cage site) to simulate the controlling, limiting, and loading effects of environment on metabolic scope (what we have termed "naked scope") and its conversion to growth.

Cages were 1-m-diameter by 1-m-tall cylinders made of 3-mm vinyl mesh over a polyvinylchloride-pipe frame. Cages were deployed in clusters of 6–12, with each cage spaced about 1 m from its nearest neighbor. Cages were set on end, in water 0.8 to 1.2 m deep. Thus, caged fish had access both to conditions near or at the water surface and at the substrate.

Some cages were partitioned internally, to form 4 equal, wedge-shaped cells extending from the top to the bottom of the cylinder. From 1 to 50 fish were stocked into unpartitioned cages. In trials involving partitioned cages, four fish were stocked per cage—four together in unpartitioned cages and one fish in each of the four cells of partitioned cages. Sewn into the cages' tops were one or four "sleeves" of plankton netting, through which feed could be inserted.

FT01. This 7-day cage trial in the Packery Channel area during September 1998 involved very small red drum, which weighed just over 0.1 g each at stocking. Water temperature ranged approximately from 27 to 34°C, with more than 75% of recorded values between 29.2 and 30.5°C (FT01PCNom.stm and FT01PINom.stm). Natural forage, consisting mostly of microcrustaceans and postlarval grass shrimp, was put into the cages daily. Apparent mortality rates of the fish were high at both of two field sites. At the PC site, only 11% of

stocked fish were recovered, but surviving fish increased in weight, from 0.146 to 0.192 g (medians). At the Padre Isles site (PI), survival was slightly greater, at 16%, but survivors apparently lost weight, from 0.128 to 0.122 g (medians).

Because this cage trial was so brief, the simulation was extended backward in time, to include the 5-day period just prior to stocking the cages. The goal was to have the simulated fish start the experimental period not only with the correct weights, but also with the appropriate states of temperature and DO acclimation. This was accomplished by using pretrial environmental data from their culture pond (at the Perry R. Bass Marine Research Center, Palacios, TX) and by finding, via trial-and-error, the weights at time-5 days that gave the observed median weights at time-zero.

The value of MMSO required to give a perfect fit for the PC data was 0.312 (FT01PCNom.stm), which is consistent with MMSOs from the parameterization trials with larger juvenile red drum. But using the same value of MMSO for PI (FT01PINom.stm) caused substantial overestimation of weight change there—+1.00%/day, vs. −0.67%/day observed. The weight change discrepancy at PI can be accounted for fully, in two ways: 1) MMSO at PI was only 0.241, owing to deteriorated quality of habitat there (FT01PIOptMMSO.stm); 2) MMSO was the same at PI as at PC, 0.312, but vertical stratification in this bulkheaded canal caused ambient DO where the fish spent most of their time (presumably, hiding at the cage bottoms, in the loose mat of the seagrass *Halodule* that had been introduced to provide cover and retain forage) to be only 60% of that recorded by the environmental probe positioned about 20 cm off the bottom, in open water (FT01PIOptDO.stm).

Under the nominal model, MORT*100% at the end of the trial was 88 and 40% for the PC and PI sites, respectively; the corresponding values of observed mortality rate were 89 and 84%. MMSO optimization of the simulation for PI left MORT unchanged, at 0.40; but, DO optimization resulted in a *decrease* in MORT at PI, to 0.17. This result (i.e., decreased rate of low-DO mortality with reduced DO) seems, at first, paradoxical. However, close comparison of the output from FT01PINom.stm and FT01PIOptDO.stm indicates that the supposed reduction in DOa, under FT01PIOptDO.stm, enhanced downward DO acclimation during the first night of exposure to PI's low DO, providing some improvement in lethal resistance when DOs went even lower the second night. This kind of response from Ecophys.Fish is another example of its conceptual consistency with expected (if somewhat counterintuitive) patterns: Acclimation complements "anticipatory adjustments" (Fry, 1947, 1971) such as those cued by photoperiod and mediated by the endocrine system, to position the animal's physiological state optimally, relative to likely future trajectories of the environmental regime. If the future course of joint environment is one of improvement, no harm is done. But if the future brings further environmental deterioration, acclimation improves chances for averting disaster.

Combinations of reduced MMSO and lesser DO limitation also could account for the weight change rate at PI—and perhaps give a value of MORT in better agreement with the observed mortality rate. But, these more complex scenarios were not explored.

PT01. In this late-winter trial lasting 32 days, 24 red drum with initial weights from 32 to 210 g were caged individually in an MDC pond and fed shrimp meat at rates of 1, 6, and 10% of initial weight per day. Pond temperature ranged approximately from 11 to 24°C, with 75% of recorded values between 16.7 and 21.3°C (PT01Nom.stm). With an MMSO of 0.305, the nominal model (PT01Nom.stm) accounted for 84% of the variation in weight-change rates of the individual fish, and clearly resolved the three treatment groups (Figure 10a). However, the model progressively underestimated Wchg as ration declined.

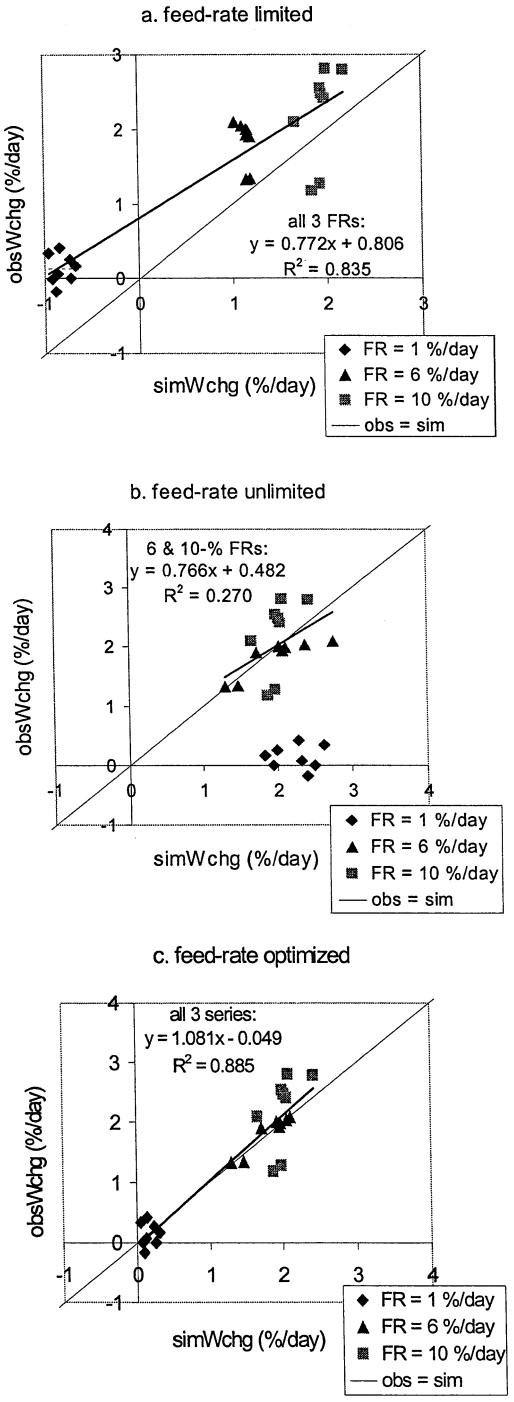

Figure 10. Observed vs. simulated rates of weight change, field trial PT01, under feed rate (a) limited and (b) unlimited versions of the nominal red drum model (PT01Nom.stm), and under (c) the feed rate optimized model (PT01Opt.stm). MMSO = 0.305, in each case.

Replacing the nominal model's assumption that feed was limited to the provided ration, with one invoking unlimited feed, made evident the likelihood that the 6 and 10%/day treatment groups achieved a maximum daily ration; whereas, the 1%/day treatment group did not (Figure 10b). Trial-and-error fits of the model with "natural," 1,000-cal/g forage in the pond assumed to supplement the provided ration (PT01Opt.stm) suggested that PT01 red drum fed 1, 6, and 10%(Wo)/day may have acquired an additional ration of 2.5, 2.3, and 2.3%(W)/day from forage in the pond. This optimized model (PT01Opt.stm), with MMSO = 0.305, accounted for almost 89% of the variation in Wchg of individual fish, and the regression of obsWchg on simWchg had slope and intercept very near 1 and 0, respectively (Figure 10c).

PT02. This 33-day MDC pond trial followed PT01 by about 1 month, and it involved smaller fish—4 to 16 g, initial weight. Pond temperature ranged approximately from 18 to 29°C, with 75% of recorded values between 21.2 and 25.7°C (PT02Nom.stm). Individually caged fish were fed shrimp meat at 5, 10, or 15% (Wo)/day; of nine fish allocated to each feeding-rate treatment, numbers surviving the entire trial were 9, 7, and 8, at feeding rates 5, 10, and 15%/day, respectively. The obsWchg data suggested no difference among feeding rate treatments, in marked contrast to results simulated under the nominal model with feed limited to that provided (PT02Nom.stm; Figure 11a). Clearly, the combination of smaller fish, more advanced warm season with commensurate increase in forage production, and greater minimum rate of feed application for PT02, relative to PT01, made for ample feed intake, even at the lowest rate of feed application. And, in fact, the assumption of unlimited feed gave values of simulated Wchg quite consistent with the observed values (Figure 11b). That the coefficient of determination was no higher than 0.64 could be attributed more to the small range in Wchg, than to any systematic lack-of-fit on the part of the model. Optimum value of MMSO seemed to be 0.305—the same as in PT01.

PT03-24g vs. PT03-24b. The intent of this pair of 14-day trials during fall 1999, was to contrast performance of juvenile red drum caged in "good" (PT03-24g) and "bad" (PT03-24b) subhabitats within the same pond, pond 24 at MDC. Pond temperature ranged approximately from 17 to 25°C, with 75% of recorded values between 20.0 and 23.0°C (PT03-24gNom.stm and PT03-24bNom.stm). The "good" subhabitat was flushed with aerated water continuously discharged by a paddlewheel aerator; whereas, the "bad" subhabitat was in slack water. In each subhabitat, there were two feeding rate treatments—finely-minced shrimp meat at 20%(W)/day vs. no feed—and two levels of separation among fish—each of four individuals per cage in its own quarter-cage compartment, and four individuals together in a noncompartmentalized cage. Fish were about 0.3 g, initially. Fish were habituated to the cages for the first 3 days of the trial, before initial weights were obtained. Therefore, trial-and-error simulation over the pretrial interval was performed to find day-3 weights that would give the observed starting weights and presumed acclimation states on day 0 (same procedure as in FT01 simulations above).

Values of obsWchg suggested 40% faster growth in the "good" subhabitat. In neither subhabitat was there a clear difference in Wchg between feeding treatments or between individual separation treatments.

Because the unfed and fed fish in both subhabitats achieved similar rates of growth, feed-limited models were rejected in favor of their feed-unlimited variants. Thus, we set FeedRate to 1, a value well in excess of any possible demand. (The actual FeedRate at which Ecophys.Fish declares a feed limitation under the fish size, feed, and environmental conditions of PT03-24 is 0.20 to 0.25 (20–25%W/day), depending on initial Wfish.) We

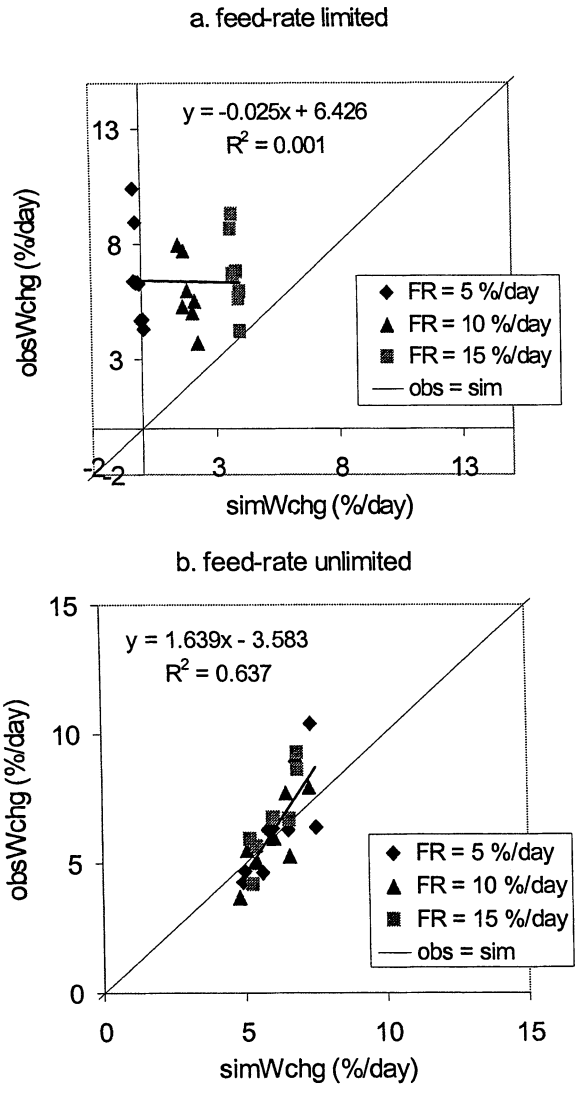

Figure 11. Observed vs. simulated rates of weight change, field trial PT02, under feed rate (a) limited and (b) unlimited versions of the nominal red drum model (PT02Nom.stm). MMSO = 0.305, in each case.

began the effort to simulate growth by invoking the assumption that the consumed feed provided the fish 1,000 cal/g. With MMSO reduced to 0.290—reduced from the value we had come to consider nomimal, 0.310—the model fit the central tendency in growth observed in PT03-24b. But, the model undersimulated growth in PT03-24g, no matter how high the value of MMSO was set. So we adopted MMSOs of 0.310 and 0.290 as appropriate for the nominal PT03-24 simulations (PT03-24gNom.stm and PT03-24bNom.stm, respectively) and accepted the assessment of obsWchg-simWchg relationships reflected in Figures 12a and 12b—given GEfeed = 1,000 cal/g.

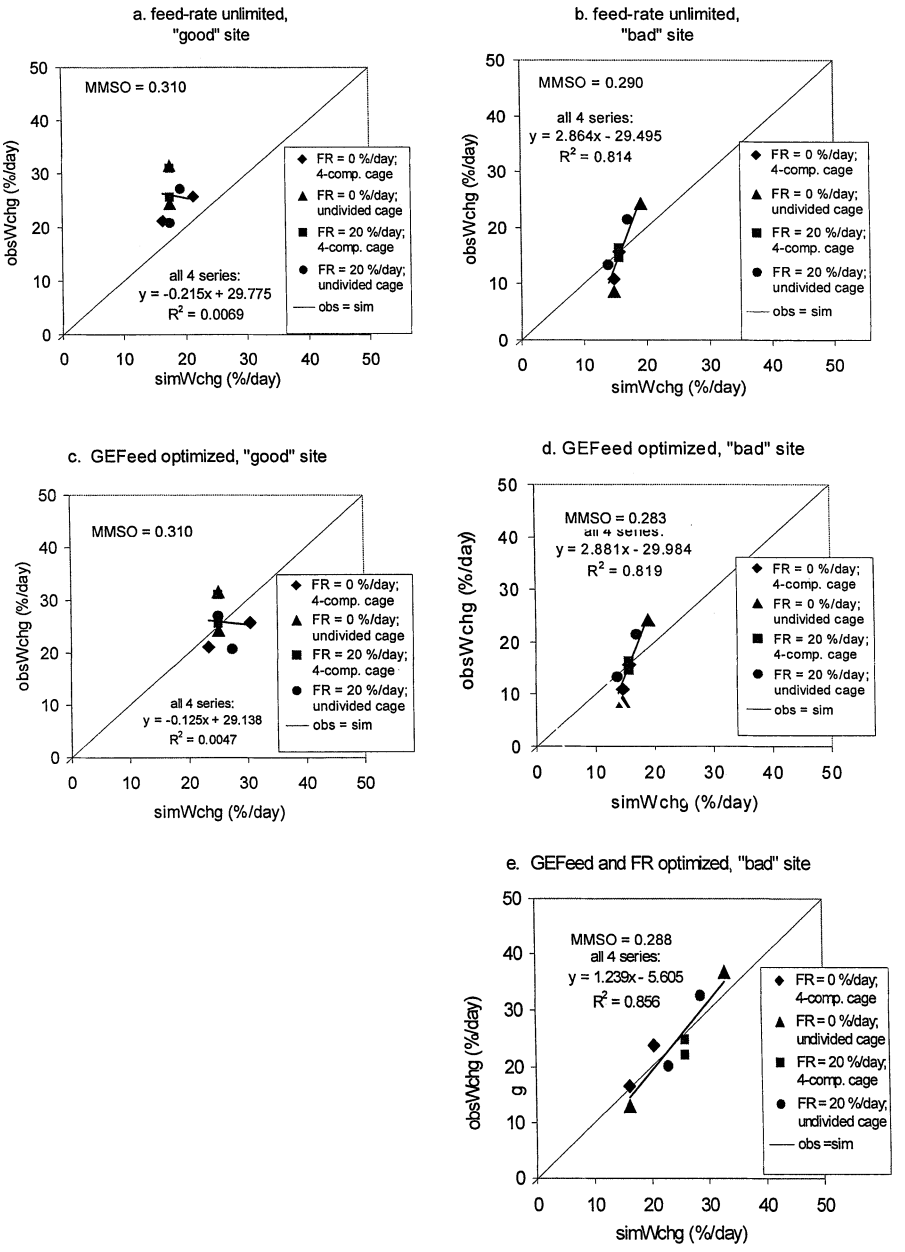

Figure 12. Observed vs. simulated rates of weight change for red drum in field trial PT03 at "good" (PT03-24g) and "bad" (PT03-24b) sites, under the nominal red drum model with unlimited feed rate (a, PT03-24gNom.stm; b, PT03-24bNom.stm) and under the same model except optimized by setting GEfeed to 1,200 cal/g (c, PT03-24gOptGEfeed.stm; d, PT03-24bOptGEfeed.stm). Remaining systematic lack-of-fit at the "bad" site (d) was largely resolved by invoking additional optimization of feed rate and GEfeed as a function of fish weight (e, PT03-24bOptGEfeedFR.stm; see text).

But why restrict GEfeed to 1,000 cal/g? Although the shrimp meat we fed had about that caloric density, clearly the unfed fish were eating something other than what we fed them; maybe, the fed fish were too. So, we tried increasing GEfeed and, at 1,200 cal/g, with MMSO = 0.310 and 0.283 for PT03-24g and PT03-24b, respectively (PT03-24gOptGEfeed.stm and PT03-24bOptGEfeed.stm), both clusters of obsWchg-simWchg data moved onto the line of perfect agreement (Figures 12c and 12d).

But, for the "bad" subhabitat, there remained a striking tendency for within subhabitat correlation between obsWchg and simWchg values ($R^2 = 0.82$; Figure 12d); this correlation seemed traceable to differences in median initial weight of fish used in the eight experimental units—despite the fact that the range in median initial weight was only 0.2 to 0.4 g. For the PT03-24b dataset (but not for the PT03-24g dataset), most of the seemingly explainable variation remaining in obsWchg was accountable under a model with MMSO = 0.288 that invoked the following rule (PT03-24bOptGEfeedFR.stm; Figure 12e):

$$\text{IF Wfish} \leq 1 \text{ THEN GEfeed} = 1200 \text{ ELSE } 1000; \quad \text{and,}$$

$$\text{IF GEfeed} = 1200 \text{ THEN FeedRate} = 1 \text{ ELSE}\{0.0, 0.2\}.$$

That is, fish weighing less than 1 g obtained a maximum ration from natural forage with 1,200 cal/g; but once fish exceeded 1 g (and became too large to consume the small, energy-rich forage?), they ate only the 1,000-cal/g shrimp meat (if) provided. Both because we can offer no empirical evidence to support this complex rule and because it does not work to explain variation in the PT03-24g dataset, we withdraw to the speculative front comprising PT03-24gOptGEfeed.stm and PT03-24bOptGEfeed.stm (Figures 12c and 12d).

Both observed and simulated results indicate that 24g did, in fact, constitute superior habitat, relative to 24b, for these small red drum. The fish in 24g grew at about 26%/day; whereas, those in 24b grew only at about 16%/day. Under Ecophys.Fish, this difference corresponded with a marked difference in MMSO: Taking MMSO for 24g to be the nominal value, 0.31, the value for 24b was only 0.283. The fact that different MMSOs were required to account for the difference in fish performance indicates that the environmental differences between 24g and 24b went beyond those attributable to the modeled effects of temperature, DO, salinity, and pH.

PT04. This 13-month MDC pond trial involved six cages, each with an individual red drum fed daily to satiation with shrimp meat. The experiment began in March 1999 and terminated in April 2000. At approximately monthly intervals, the individual fish were removed from their cages and weighed, the cages cleaned, and the fish replaced. One fish died and two others escaped during the monthly maintenance process. The three fish that lasted the entire 13 months weighed 13.2, 13.7, and 14.7 g when the trial began, and 1281, 1526, and 1292 g, respectively, when it ended.

Temperature, DO, salinity, and pH were measured three times each day about 20 cm above the pond bottom at the cage site, using a hand-held YSI 85 multi-environmental meter and probe. The environmental variables exhibited typical diel and seasonal trends, with the diel variation in DO being especially prominent (Figure 13a; PT04Nom.stm).

The ecophysiological model (PT04Nom.stm) with MMSO set to 0.320, generated a growth curve generally similar to those produced by the real fish, especially before the trial's final month (Figure 13b). But during that final month, the model fish obviously outgrew the real fish—and even before that, the model exhibited some lack-of-fit, but in the opposite direction. We found two ways to account for these discrepancies: 1) PT04OptWinMMSO.stm; Figure 13c: The real fish had routine metabolic rates that were 5% lower than those presumed

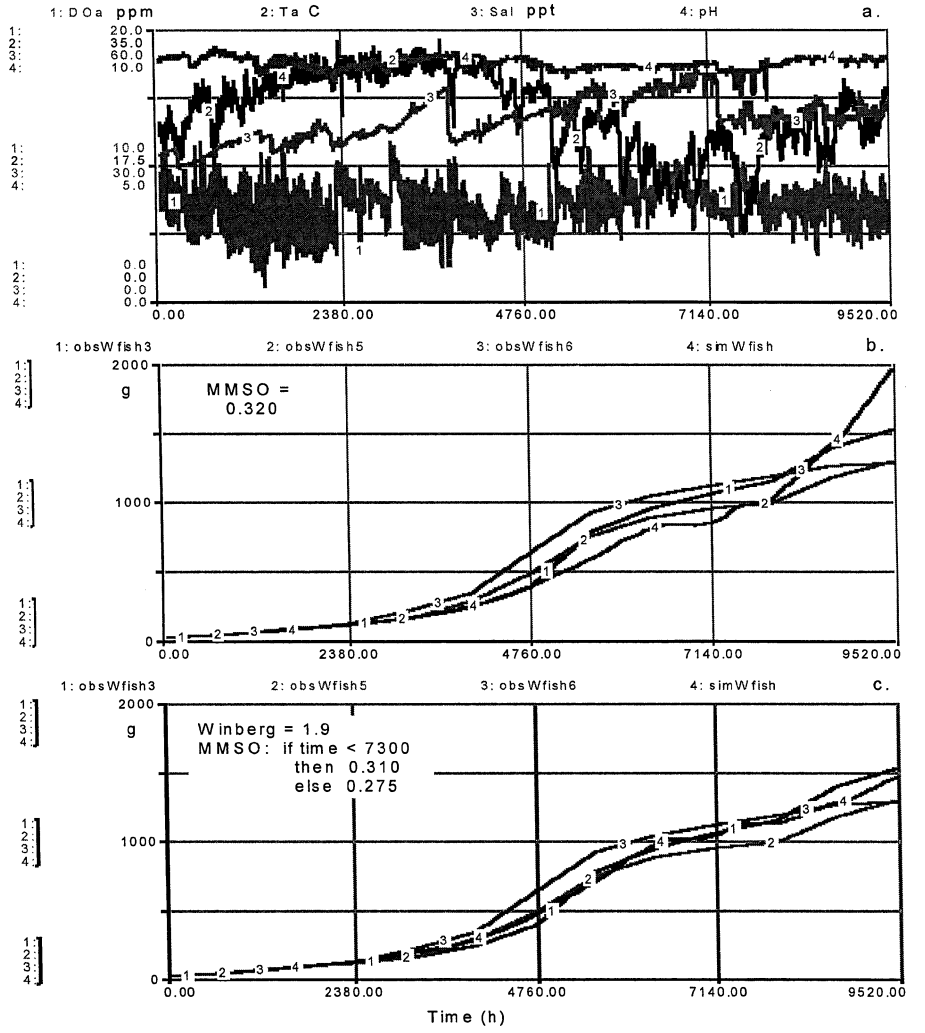

Figure 13. Environmental conditions during 13-month field trial PT04 (a) and observed weights of three caged red drum vs. those simulated under the nominal model (b, PT04Nom,stm) and the Winberg/MMSO-optimized model (c, PT04OptWinMMSO.stm).

under nominal Ecophys.Fish—thus, the Winberg parameter needed reduction from 2.0 to 1.9—and in late January 2000 (at hour 7300), their MMSO deteriorated from its previous value, 0.310, to 0.275 (instead of being always at the constant value, 0.320, supposed under PT04Nom.stm). In potential support of the hypothesized change in MMSO, it can be noted that at about the same time it was presumed to have occurred, pond salinity underwent an abrupt 10-ppt reduction, from 50 ppt to 40 ppt, and water temperature fell several degrees (Figure 13a), as a late-season cold front brought heavy rains and frigid conditions to the Corpus Christi area. The salinity reduction per se should have improved fish performance (as, in fact, it did, under the nominal model); that it did not, would suggest some collateral deterioration in water quality accompanying the change in water mass. (In fairness, it must be noted that pond salinity underwent a similar change at about hour 3800, with no apparent

effect on fish performance). 2) PT04OptWinFR.stm: Again, Winberg was reduced to 1.9, but MMSO was constant throughout the trial, at 0.310. As the fish exceeded about 1 kg in weight, at hour 7300, it became impractical to provide enough shrimp meat to satiate them; and, so, after hour 7300, FeedRate achieved by the fish was reduced to 0.45 of FeedRateMax. The model invoking a reduction in FeedRate gave virtually the same values of simWfish as that invoking a reduction in MMSO. We prefer the MMSO reduction explanation.

For Wchg values reckoned over the 13-month trial's six consecutive 66-day intervals (and using the "running start" initialization procedure described above for MidaHumberto.stm), Ecophys.Fish was able to account for 92% of the variation in weight-change rate (averaging for the three fish)—even without optimization (Figure 14a; PT04Nom.stm). With optimization (of either type), the coefficient of determination for 66-day Wchg increased to about 96% (Figure 14b; PT04OptWinMMSO.stm).

PT04 was the one field trial other than FT01 to register a nonzero rate of simulated mortality: Under PT04Nom.stm, terminal MORT was 0.06, which corresponds with a simulated mortality rate of 6%. The observed rate of known mortality was 1/6, or 17%. But as indicated above, the one death that actually occurred was probably caused by handling, not by the low DO responsible for the simulated mortality.

CPL Trial. This 17-day cage trial was performed during February 2001, in heated and ambient areas of the cooling reservoir of Barney Davis Steam Electric Power Plant, operated by Central Power and Light Co., at Flour Bluff, TX. Water at the ambient cage site began the trial at about 15°C, rose to 25°C midway through the trial, declined abruptly back to about 15°C, then rose again, to near 26°C at the trial's end. The thermal regime of the heated cage site was typically about 2-°C warmer than at the ambient cage site. In addition to the heated/ambient-subhabitat treatment, there were two feeding rate treatments—shrimp meat at 2 and 15%(W)/day—and two levels of separation among fish—each of four individuals per cage in its own quarter-cage compartment, and four individuals together in a noncompartmentalized cage. Fish were about 8 g, initially.

In this trial, an effort was made to estimate MMSO empirically, via automated respirometry performed on a sample of fish at the trial's termination. Eight fish—two from each of two noncompartmentalized cages fed at 15%(W)/day in each subhabitat—were used in respirometry. Seven of these fish, three from the ambient area and all four from the heated area, yielded MMSO estimates. MMSO values were estimated from respirometry data by using the nominal ecophysiological model, replete with environmental data both from cage and respirometer phases, to find that MMSO value giving a simulated terminal MMS equal to the value observed in respirometry (Figure 15). For each of the seven fish, simulated Wchg was computed under the model with the constraints that at the termination of respirometry, 1) DOa = LOCr, 2) VO2 = RMR = Mact, and 3) simMMS = obsMMS. For six of the seven fish, there existed a MMSO that permitted all three constraints to be met. But for one fish from the heated subhabitat, no MMSO could be found that allowed both the VO2 and MMS constraints to be satisfied. In this case, it was necessary to relax the assumption that Winberg = 2, instead increasing the value of this parameter to a minimum of 2.20. The interpretation of this development is that this fish's activity component of metabolism must have been elevated, relative to standard metabolism, by 20% over the comparable figure for the other six fish. Why the one fish might have been aberrant is not evident. It may be noted that its MMSO, at 0.284, was at the median for its group. However, it may also be noted that this was the one fish among the four tested from the heated subhabitat that had minimal weight gain.

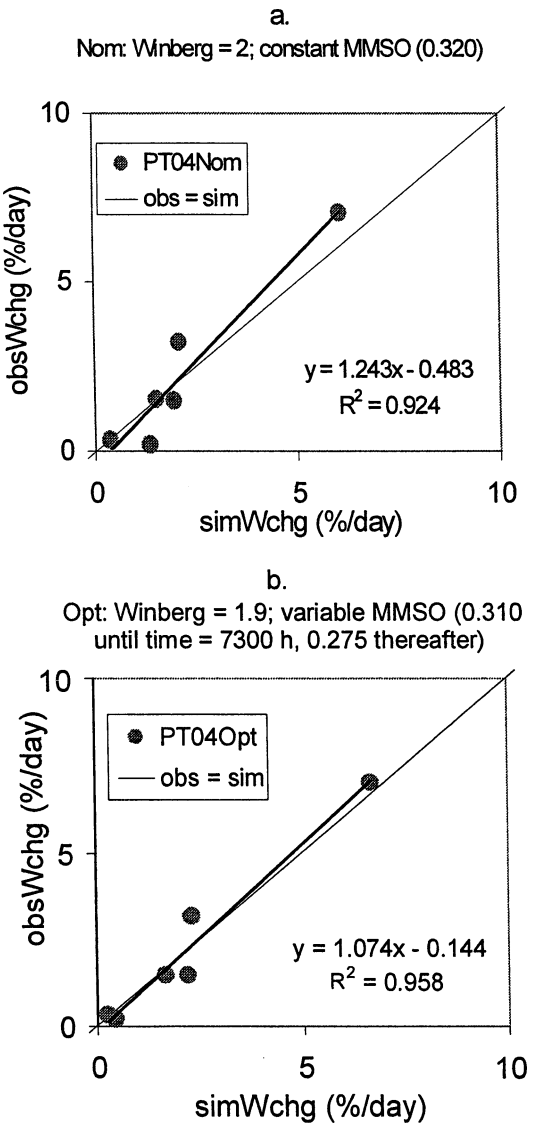

Figure 14. Observed vs. simulated rates of weight change over 66-day intervals, for field trial PT04, under the nominal red drum model (a, PT04Nom.stm) and under the Winberg/MMSO-optimized red drum model (b, PT04OptWinMMSO.stm).

MMSOs for heated-subhabitat fish ranged from 0.246 to 0.298, with a median of 0.284; thus, empirically estimated MMSOs for this group were not especially extreme, relative to those estimated by goodness-of-fit in the other trials. However, two of the three ambient-subhabitat fish had MMSOs that tended to be well below those estimated in the other trials; MMSOs for the three ambient-subhabitat fish were 0.198, 0.211, and 0.284.

With these empirical estimates of MMSO, the ecophysiological model did a fair job of simulating Wchg for the CPL trial, and the model properly resolved the apparent

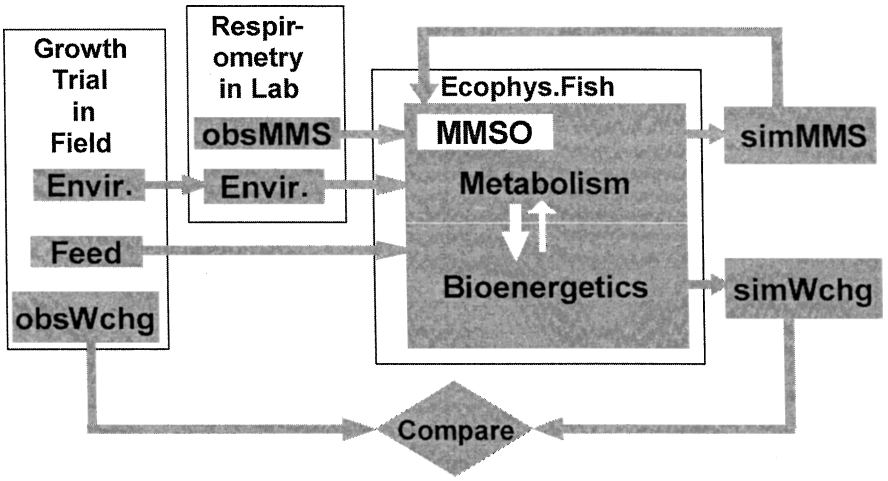

Figure 15. Using respirometry data to estimate Ecophys.Fish's MMSO parameter, for evaluation of fish growth in associated field trials.

effect of subhabitat on Wchg (Figure 16a). A comparison of the empirical MMSOs with those required for perfect Wchg fit (Figure 16b) provides evidence both for the model's overall reasonableness and for validity and relevance of our respirometric estimates of MMSO.

Conclusion, Regarding Field Tests of Ecophys.Fish for Red Drum. Comparing obsWchg vs. simWchg values pooled for all seven datasets from field trials with caged red drum suggests that about 79% of the variance in obsWchg might be explained by the model (Figure 17a), even if one intentionally handicaps it by choosing, in each case, the nominal model variant giving the poorer fit to the observed values. We judge this a very respectable showing, considering that the test trials involved highly variable environmental regimes, durations from 7 days to 13 months, and fish ranging in weight over four orders of magnitude (0.1 to 1000 g). Moreover, the model was parameterized in trials involving fish fed only prepared feeds but tested in trials involving fish fed only "natural" feeds. Optimization of the model, mostly by judicious adjustment of feed inputs, increased the model's coefficient of determination to 94% (Figure 17b).

Two final points should be made regarding the apparent error in performance of the nominal model for red drum: 1) For the aggregate dataset, Ecophys.Fish undersimulated red drum growth (Figure 17a). This is what one should expect for a "naked scope" model, even if in the confinement of cages, the fish were able to exploit directive factors to their growth advantage. And, in fact, when one examines the optimizing adjustments that led to substantial improvement in model performance (Figure 17b), several have to do with presumed selection of microhabitat (within the cages) or forage. 2) Perhaps, the present version of Ecophys.Fish is simply inadequate to represent the ecophysiology of "growth" in very small red drum, say individuals weighing less than 1 g. We remain uncomfortable with the model's fits and our optimization arguments for trials PT03-24g and PT03-24b. Fish as small as those used in these trials—0.2 to 0.4 g—may still be undergoing development from larva to juvenile, as distinct from juvenile growth. None of our parameterization

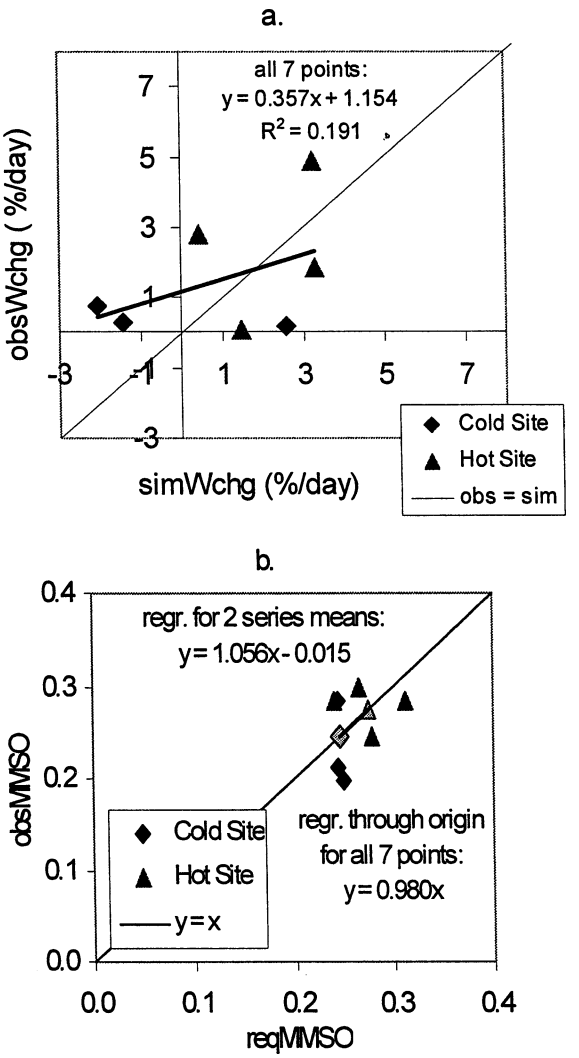

Figure 16. Observed vs. simulated rates of weight change (a), and observed vs. required values of MMSO (b), under nominal model, in CPL field test with red drum.

trials involved fish that small. Thus, some of the rules invoked by Ecophys.Fish may not apply.

Probably the wisest course, given current information, is to exclude from model evaluation the field trials that involved red drum with initial weights less than 1 g (FT01, PT03-24g, and PT03-24b). And in the same conservative spirit, let's compromise between "pessimistic" and "optimistic" comparisons, and settle on what we might call a "sensible" comparison: for only those trials involving fish with initial weights exceeding 1 g, simWchg under the nominal model with FeedRate set to 1 (unlimited) vs. obsWchg restricted to that treatment within trials PT01, PT02 and CPL that involved the highest rate of feed application (already the PT04 data were for fish fed to satiation). The picture that

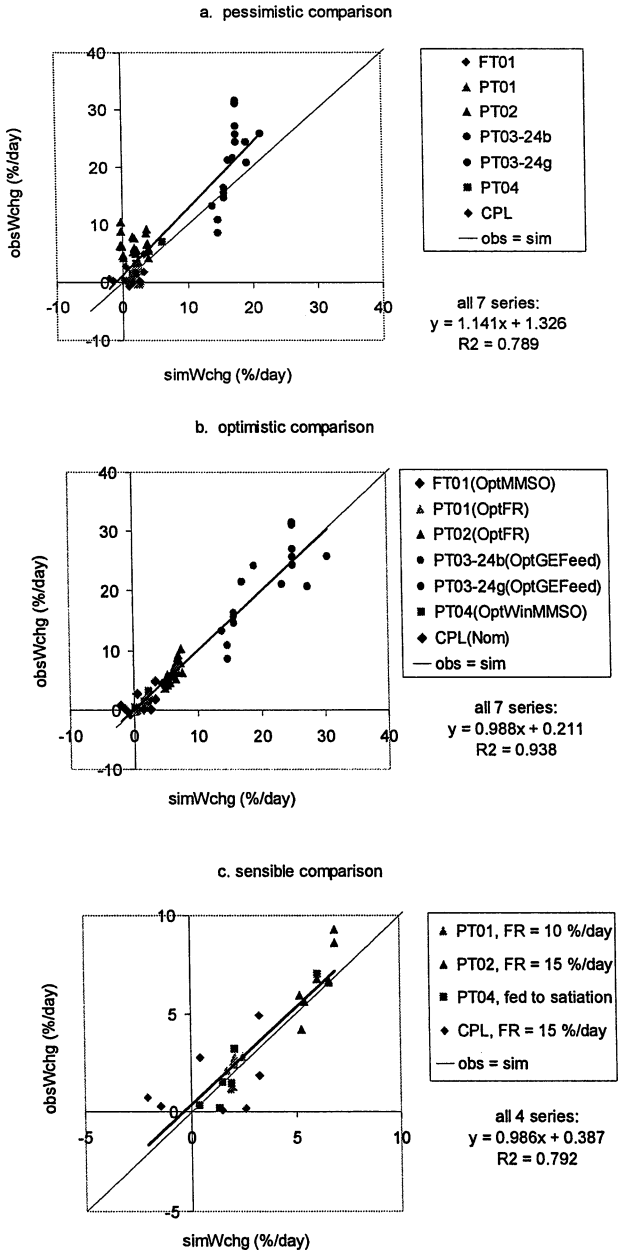

Figure 17. Three comparisons of observed vs. simulated rates of weight change, in seven field tests of Ecophys.Fish for red drum: (a) Pessimistic comparison—values of simWchg are those simulated under the nominal model, or its variant giving the *poorer* fit. (b) Optimistic comparison—values of simWchg are those simulated under the model optimized as indicated. (c) Sensible comparison—in the four field trials involving red drum with initial weights greater than 1 g, values of simWchg are those simulated under the nominal model with FeedRate set to 1 (unlimited); values of obsWchg are those from the treatment involving the highest rate of feed application.

emerges (Figure 17c), although far from perfect, is quite satisfactory, we think: Slope and intercept of the obsWchg-simWchg relationship are 0.986 and 0.387, respectively; and R^2 is 0.792.

Extension of Ecophys.Fish to Bluegill

Using Caged Bluegill to Ecoassay Urbanizing Streams in San Antonio, TX

The bluegill (*Lepomis macrochirus*) is a well-studied member of the sunfish family (Centrarchidae). It is native to eastern North America, where it occurs in freshwater streams, lakes, and impoundments. Seldom exceeding a weight of 0.5 kg, the bluegill feeds mainly on zooplankton and aquatic invertebrates. This sunfish is a popular sportfishing target and is widely used in research on fish biology and aquatic ecology.

Beginning in late summer 1999, a Texas A&M research team led by Neill performed a series of ecoassays using caged bluegill to assess impacts of urbanization on streams of Texas' upper San Antonio River basin. The resulting data on stream environment, bluegill growth, and bluegill metabolic performance (Fontaine, 2002) provided opportunity—and owing to some uncertainty about the meaning of the data, the motivation—for an independent application of Ecophys.Fish.

We exposed juvenile bluegill (initial weight, 7–20 g), each confined to a $30 \times 30 \times 30$ cm^3 cell within a floating cage of 0.8-cm plastic-coated wire mesh, to in-stream conditions at two sites in each of two streams—Leon and Salado creeks—during Summer 1999, Summer 2000, and Winter 2000 (the "Winter 2000" ecoassay extended from December 2000 into January 2001). For each of the 12 stream-site, season/year combinations, we successfully measured MMS via respirometry for four to nine of the 12 individual fish, at termination of their 10–23 day exposure periods; we then compared the 12 median values of MMS and estimated MSgrowth with the corresponding medians of Wchg. Median MMS accounted for 35% of the variation in median Wchg (Figure 18a). When MMS and VO2r were transformed to their MSgrowth equivalent (Neill and Bryan, 1991)

$$\text{MSgrowth(estimated)} = \text{MMS}^{*}\text{DO} - \text{VO2r},$$

at DO = 3.0 mg/L, median MSgrowth accounted for 41% of the variation in Wchg. Finally, when MMS and VO2r were adjusted for the expected effects of median in-stream temperature (Ta), the percentage of variation in median Wchg accounted for by Ta-adj. MSgrowth increased to 47% (Figure 18b). The regression of Wchg on Ta-adj. MSgrowth had an intercept of -0.40 and a slope of 8.66. We interpret these regression coefficients to mean that the metabolic scope necessary for weight maintenance of our San Antonio bluegill was about $0.40/8.66 = 0.05\ \text{mgO2} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$, and that above this maintenance value, about $1/8.66 = 0.12\ \text{mgO2} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ of metabolic scope was required for each $1\% \cdot \text{day}^{-1}$ change in body weight.

It is of interest to ask, "What might have been the metabolic expenditures of the fish while in the cages relative to those in the respirometers?" If one assumes the caged fish used all their metabolic capacity (at DO = 3 mg/L), then they must have expended about 40% more in routine metabolism in-stream than in the respirometers—i.e., the median values of Ta-adj. VO2r used to compute Ta-adj. MSgrowth must be multiplied by 1.4, to shift the regression equation's intercept from -0.40 to zero.

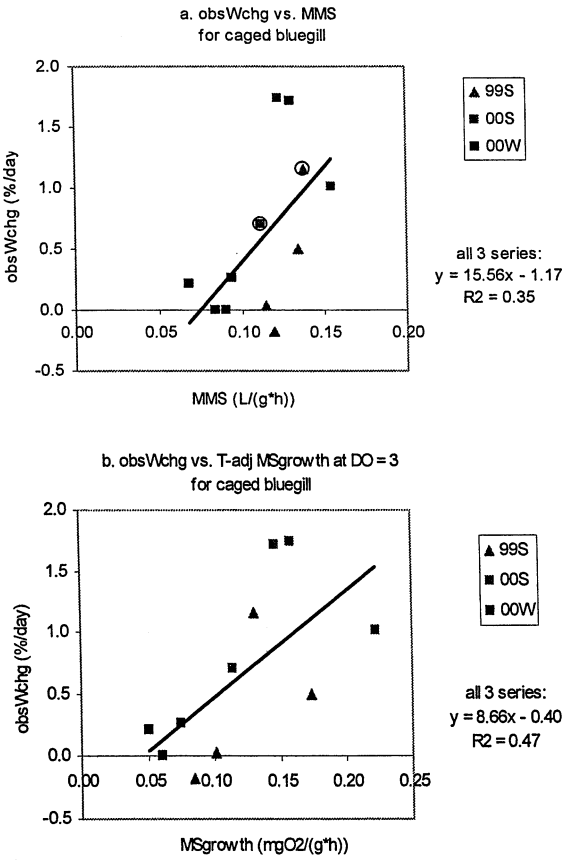

Figure 18. Median rates of weight change for bluegill caged in streams vs. their medians of marginal metabolic scope (MMS) measured subsequently in the laboratory (a), and projected values of metabolic scope for growth (MSgrowth) at median stream temperature and DO = 3 mg/L (b). In panel a, encircled points are two cases for which there were incomplete environmental data; R2 for remaining 10 points is 0.31.

Parameterization of Ecophys.Fish for Bluegill

The foregoing analysis of the bluegill ecoassay data, while instructive, was less than gratifying, both because more than half the variation in median Wchg remained unexplained, and because only a small fraction of the explained variation could be attributed to variation in the components of stream environment that we measured. But up to this point, our attempt to explain the variation in weight change rate observed for bluegill caged in San Antonio streams had not involved the ecophysiological model—because there was not one for bluegill.

This we set about trying to remedy. First, the red drum version of Ecophys.Fish was reparameterized in the obvious way (given that the red drum is a euryhaline fish and the bluegill is a freshwater fish): SalOpt was changed from 10 to 0.5 ppt, and SalUL was changed from 50 to 10 ppt (Peterson and Meador, 1994). Then, Smino (the ultimate intercept of standard metabolic rate) was reduced from 0.1 to 0.02 mgO2/(g*h), and the maximum value of DOlim was reduced from 8.5 to 6 mg/L, to give metabolic relations that are in

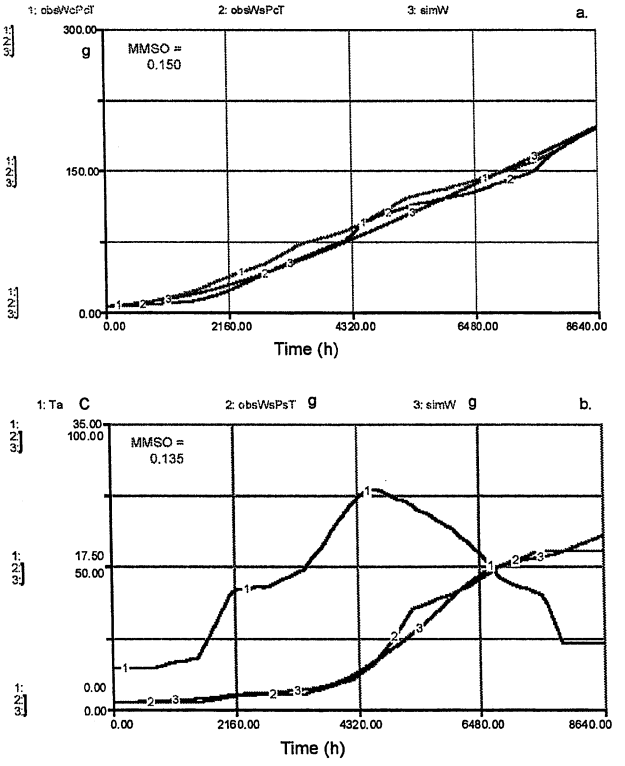

Figure 19. Ecophys.Fish fitted to McComish's (1971) constant-temperature (a) and seasonal-temperature (b) growth trials with bluegill. Key to suffix codes: cP = constant photoperiod; sP = seasonal photoperiod; cT = constant temperature (21°C); sT = seasonal temperature.

general conformity with findings of Pierce and Wissing (1974). These adjustments and a few others made, the model seemed to be fitting our bluegill data—at least those in hand at the time (Fall 2000). But then we obtained a copy of McComish's (1971) dissertation, and found that more substantial revision of the model was required to fit those data. Finally, without having done any parameterization trials of our own, we arrived at a nominal version of Ecophys.Fish that gave an acceptable fit to McComish's (1971) bluegill growth trials (Figure 19a, McComishCT.stm; Figure 19b, McComishST.stm), and accounted for about 85% of the variation in median Wchg of bluegill we observed in our San Antonio stream ecoassays. Thus, the bluegill version of Ecophys.Fish would have seemed, on that basis, to be at least the equal of the red drum version. But systematic lack of fit in simWchg suggested underlying problems with the bluegill version of the model, the San Antonio bluegill data, or both (see below, p. 272).

The lethal effect of low DO was parameterized using the mortality data from 10 of the 12 groups of bluegill caged in the San Antonio streams (2 of the 12 stream-site-year/season environmental datasets had been lost, owing to environmental datalogging failure). Observed mortality ranged from 0 to 45%; simulated mortality ranged from 0 to 80%. Excluding the winter data, when mortality was not associated with low DO, the model's fit was respectable: R^2 for a plot of the six pairs of mortality probits was 0.684 (Figure 20).

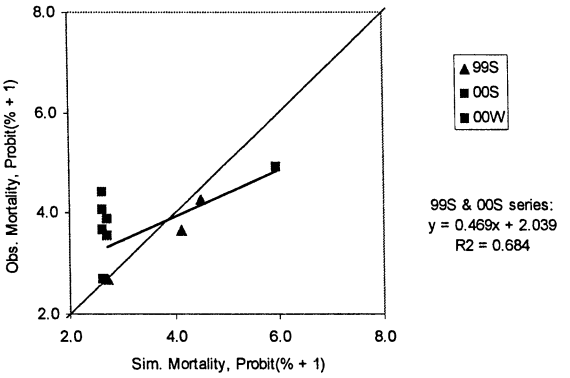

Figure 20. The fit of Ecophys.Fish to mortality of bluegill caged 13–22 days in San Antonio, TX, streams.

Table 2 lists the names and values of all the parameters that differ between the current red drum and bluegill versions of Ecophys.Fish. Of the model's total parameter set—about 40, depending on how one counts—only 18 are different (at the species level) and thus, appear in the list.

Table 2
Parameters that differ between red drum and bluegill versions of Ecophys.Fish. Not included are MMSO and Winberg, which are input variables that tend to differ among growth trials and individual fish

Parameter	Dimensions	Red Drum Value	Bluegill Value
SalOpt	ppt	10	0.5
SalUL	ppt	50	10
Topt	°C	28	30
Taccl, minimum for nil Ta*Sal effect on Smin	°C	18	12
Taccl, maximum	°C	34	35
Tinfl	°C	32	28
q1	1/°C	0.05	0.07
Hill	(dimensionless)	2	4
DOlim, intercept	mgO2/L	0.35	0.8
DOlim, maximum	mgO2/L	8.5	6
Smin0	mgO2/(g*h)	0.1	0.0167
GEfish, minimum	cal/g	800	700
GEfish, maximum	cal/g	1400	1100
FeedRateMax, W = 1 intercept	g-feed/(g-fish*day)	0.18	0.23
FeedRateMax, W-power, LnW intercept	(dimensionless)	−0.25	−0.52
FeedRateMax, W-power, LnW slope	(dimensionless)	0.0105	0
DOstress, threshold for MORT inc	mgO2/L	−2.45	−2.3
MORT inc, incrementation rate constant	L/mgO2 (per hour)	0.023	0.025

Wchg vs. MMSO in Bluegill: Using Ecophys.Fish to Improve Explanation of Growth Variation

The newly developed bluegill version of Ecophys.Fish was engaged in the process of Wchg evaluation for the San Antonio ecoassay by fitting it to each of the 10 available sets of environmental data and to the corresponding median value of observed MMS. Model fitting was performed by setting Wfish0 to the median initial weight of fish yielding the median MMS; setting post-cage environmental values to the medians of those measured during the respirometry sessions, including terminal DO at the median LOCr; and, solving for the MMSO giving the observed values of median MMS and median VO2r = Mact (Figure 15). The resulting set of 10 MMSOs explained 74% of the variation in the corresponding values of median obsWchg. Examination of the obsWchg vs. MMSO plot (Figure 21a) suggested that additional variation in median obsWchg was associated with some difference between fish responses in Summer 1999 and those in Summer and Winter 2000; and, in fact, exclusion of this variation via multiple regression indicated that MMSO would have explained 89% of the variation in median obsWchg, had the temporal difference not been a factor (Figure 21b).

What caused the difference in response between Summer 1999, on the one hand, and Summer and Winter 2000, on the other? Two possibilities are respirometry-system and feeding-regime changes, both of which occurred between the Summer 1999 and Summer 2000 research sessions. In Summer 1999, we used manually controlled respirometers with circulation provided by peristaltic pumps; in Summer and Winter 2000, we used

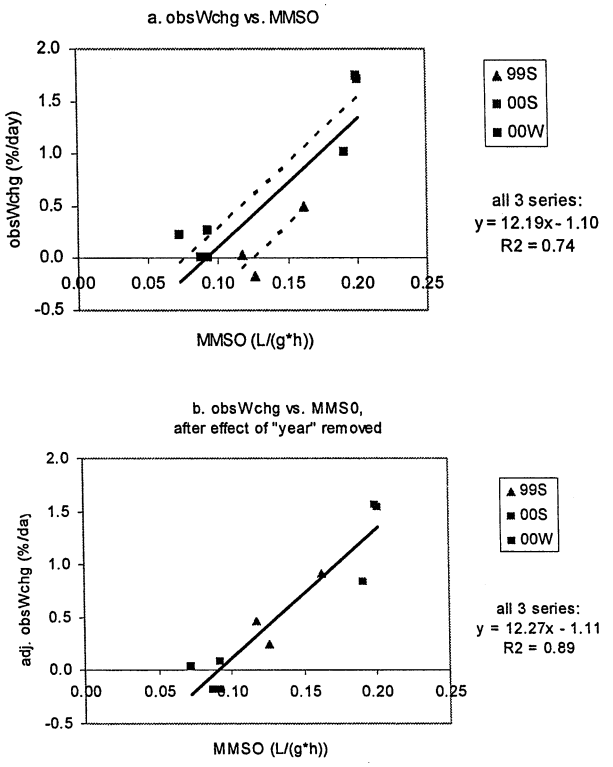

Figure 21. Median rates of weight change (a), and weight change adjusted for "Year" effects (b), for bluegill caged in streams vs. their median MMSOs estimated via respirometry and Ecophys.Fish.

computer-controlled respirometers with circulation provided by centrifugal pumps (Fontaine, 2002). But in our opinion, this difference in respirometry probably had no systematic effect on the magnitude of MMSO (and certainly could have had no effect on obsWchg). Instead, we prefer an explanation linked to the change in feeding regime. In Summer 1999, the caged fish were fed chopped, fresh earthworms to apparent satiation on alternate days; in Summer and Winter 2000, the fish were fed live mealworms to apparent satiation each day. Not only were the earthworm-fed fish fed only half as often as the mealworm-fed fish, but earthworms also have less than half the energy content (per unit live weight) of mealworms—about 770 cal/g for earthworms (French et al., 1957) vs. about 2000 cal/g for mealworms (L.P. Fontaine and W.H. Neill, unpublished data). Note that earthworm-fed fish achieved about $0.5\% \cdot \text{day}^{-1}$ less growth than did mealworm-fed fish at the same level of MMSO (Figure 21a). Although the polarity of the offset is logical, favoring the fish with the richer diet, its quantitative significance is obscured by the fact that all fish had potential access to the natural forage that may have entered their cages.

Assuming that the difference in the obsWchg vs. MMSO relationship between years was largely the difference between feeding regimes, one could interpret the progressive increase in R^2—from 0.31 for obsWchg vs. MMS (using only the 10-pair subset of data in Figure 18a for which MMSO could be computed), to 0.74 for obsWchg vs. MMSO (Figure 21a), to 0.89 for year-adjusted obsWchg vs. MMSO (Figure 21b)—as follows: Metabolic "health" of the fish at the end of the cage trial accounted for 31% of variation in obsWchg during the cage trial; physicochemical environment, independent of its effects on metabolic health, accounted for an additional 43% (74–31%); quantity or quality of feed accounted for yet another 15% (89–74%); leaving only 11% (100–89%) unaccounted for. Obviously, much of the variation both in median obsWchg and in median MMS and MMSO was seasonal, and presumably temperature related. No significant fraction of variation in median obsWchg (Fontaine, 2002), median MMS (Fontaine, 2002), or median MMSO (this analysis) could be related to differences between the two streams or to differences between sites within streams.

Median MMSO under the nominal model (Figure 21a) ranged from 0.072 to 0.189 L/(g*h). This interval includes the values of MMSO required to fit the model to McComish's (1971) data (Figures 19a and 19b) and is below the range of MMSOs found for red drum.

Observed Growth in Bluegill vs. That Simulated Under Ecophys.Fish: Conclusion

So, Ecophys.Fish can deliver estimates of MMSO that are highly correlated with recent growth rates for bluegill caged in streams. But can Ecophys.Fish accurately simulate Wchg itself? The answer to this question is, regrettably, no—not without some optimizing (and perhaps incorrect) assumptions about feeding and feed processing.

The nominal model—invoking the presumptions that the fish ate only what was fed to them and that the digestibilities of earthworms and mealworms for bluegill are 85% and 70%, respectively—produced values of simulated Wchg that were highly correlated with observed median values ($R^2 = 0.85$). However, slope of the relation between observed median Wchg and simulated Wchg was only 0.33, meaning that simulated Wchg tended to overestimate observed values by a factor of 3 (Figure 22a).

We optimized the model by assuming that the digestibility of mealworms for bluegill is only 52% (as opposed to 70%, under the nominal model); that the fish fed to satiation exclusively on the feed provided, on days when they were fed; and, that they achieved only 50% satiation on natural forage, on days when they were not fed. Thus, the average feed-forage mixture assumed was 67:33% for earthworm-fed fish, and 100:0% for

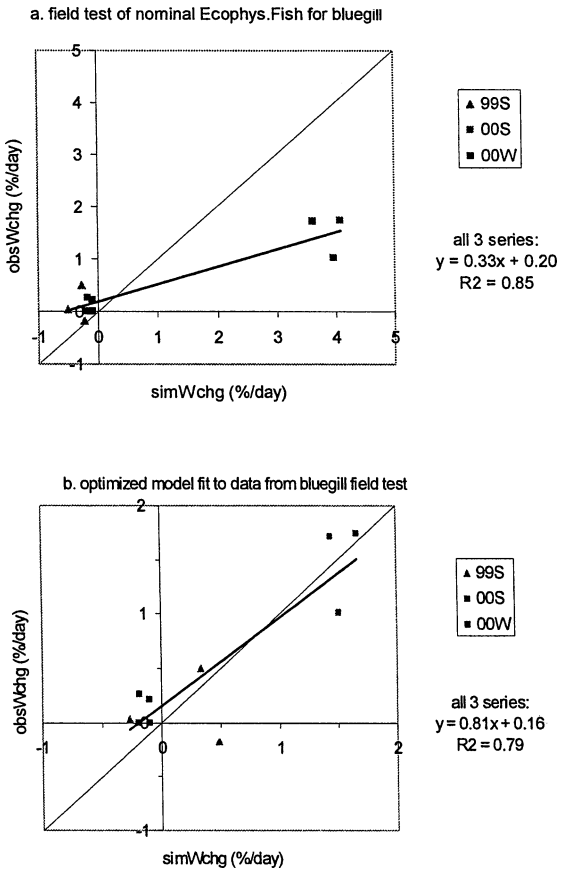

Figure 22. Observed vs. simulated rates of weight change, in field test of nominal model (a), and under the optimized model (b), for bluegill.

mealworm-fed fish. Earthworm-fed fish, on average, were 75% satiated; whereas, mealworm-fed fish were 100% satiated. Compared with the nominal model, the optimized model gave somewhat lesser correlation between observed and simulated values of Wchg ($R^2 = 0.79$), but the relationship between obsWchg and simWchg (Figure 22b) approached the line of perfect agreement much more closely than did that generated by the nominal model.

So what is the energy digestibility of mealworms for bluegill?—is it 52%, 70%, or neither? Co-authors Fontaine, Gatlin, and Neill are beginning a feeding/digestibility trial to find out. There apparently is no published value for bluegill or any other fish. Our 70% guess was based on values of gross assimilation efficiency for the lizard *Anolis carolinensis* fed mealworms (Kitchell and Windell, 1972). If that number (70%) is correct, either mealworms accounted for only about 8% of the diet of our 2000-Summer bluegill (the balance being natural forage with about 1,000 cal/g and 80% digestibility); our 2000-Summer bluegill ate exclusively mealworms but (for a reason we have been unable to guess) achieved only about half the ration consistent with their FeedRateMax; or, the parameterization of Ecophys.Fish for bluegill is seriously flawed.

If there is a serious flaw in the bluegill version of Ecophys.Fish, that flaw would seem to be centered in the bioenergetics sector, not the metabolism sector. Otherwise, MMSO would

not have accounted for such a large fraction of the variation in obsWchg (Figures 21a and 21b)—a fraction that did not change when the nominal model was replaced by the optimized model.

For both the nominal and optimized models, the values of the Winberg parameter necessary to fit MMS and VO2 = Mact simultaneously, were well above 2.0; in fact, the medians were 2.63 and 2.60, respectively. Recall that VO2r had to be multiplied by a factor of 1.4 to shift the relationship between median Wchg and temperature-adjusted MSgrowth so that its origin became zero. If VO2r in the respirometers was 2.0*Mstd, then the required Winberg factor is $2 * 1.4 = 2.8$—not too different from the values we found necessary for fitting Ecophys.Fish to the data from our bluegill ecoassay.

"Emergent" Responses of Ecophys.Fish

In the course of developing and evaluating Ecophys.Fish, we had some pleasant surprises. In the extreme, these amounted to simulated responses that, at first, seemed contrary to reason, but then upon further inspection, made sense. Already mentioned is the case of declining low-DO mortality rate with declining DO.

Perhaps more important were cases in which the model helped us to realize the obvious. One important example was this: If lethal and limiting effects of environment really are independent, as Fry (1947; 1971) suggested, then "bad" habitats for growth are not necessarily bad habitats for survival, and vice versa. Consider this hypothetical experiment: Expose two subsets of 10-g red drum for 8 weeks to identical, near-optimum environments (Ta = 28°C, Sal = 10 ppt, pH = 8), except for alternative DO treatments—1.5 ppm continuously, in one case, vs., in the other, 5 ppm DO during 95 of each 96 h but 0.75 ppm during the remaining hour. Offer both groups pelleted feed (4,000 cal/g) ad libitum. What happens? Under Ecophys.Fish (HypoDO.stm), the low-constant-DO group has high survival (100%), but a low rate of growth (0.8%/day); whereas, the group exposed to the other DO treatment has low survival (only 6%) but a high rate of growth (12.2%/day). Note that the explanation of simulated results is different from that assumed under models of density-dependence; i.e., competition for limited resources has no role in the outcome of our hypothetical experiment. This is not to say that a large biomass-density of fish (reflecting high survival and previously high rates of growth) cannot be its own cause of low DO. It is to say that for the individual fish, the source of DO limitation is irrelevant. The extent to which survival and growth operate as independent processes in real fish can be debated; but, there can be no debate about how Ecophys.Fish operates. And Ecofish.Fish is able to deliver an explicit prediction that could be easily tested by experiment.

A less obvious implication of the model is that energy-density of feed can act as a profoundly limiting factor. Although it is well documented (e.g., Brett et al., 1969) that scarcity of forage regularly limits fish growth, the notion that low energy-density of natural forage might, in and of itself, be growth-limiting seems not generally acknowledged. But under Ecophys.Fish, small red drum achieving even a "maximum daily ration" of natural forages at high temperatures are severely growth-limited by the relatively low energy-density of such feed. And, in consequence, the optimum (constant) temperature for growth of a 10-g red drum over 8 weeks is only 20.6°C, if it is fed ad libitum on 1,000-cal/g feed with 85% digestibility; the optimum increases to 28.6°C if the feed's energy-density is increased to 4,000 cal/g (GEfeed&WvsTa.stm). Again, this amounts to a testable—but, so far, untested—hypothesis.

We had expected that probing Ecophys.Fish would reveal fish size (body weight or mass) to act in a way analogous to growth-limiting environmental factors. This is because

under Ecophys.Fish, both Mact and FeedRateMax decline with increasing fish size at a greater rate than does Mstd; thus, both metabolic scope and bioenergetic scope decline as the fish grows, and could be expected to exhibit the kind of interaction typical of limiting factors with controlling factors such as temperature. Evaluation of the growth-W relationship as a function of (constant) temperature for simulated red drum fed 4,000 cal/g feed ad libitum for 8 weeks gave the anticipated, if modest, decline in optimum Ta for growth as fish weight increased—from 29.0°C for fish starting the simulation at 1 g, to 27.5°C for fish starting at 1,000 g (GEfeed&WvsTa.stm). But, when the simulation was run with GEfeed reset to 1,000 cal/g, we got another surprise: The optimum temperature increased as a function of fish weight—from 19.6°C for 1-g fish, to 27.5°C for 1,000-g fish. The reason for this reversed trend was that metabolic scope (MSgrowth) limited growth of fish at every size (over the range, 1 to 1,000 g), in the simulation with GEfeed = 4,000 cal/g; whereas, in the simulation with GEfeed = 1,000 cal/g, greatest growth for each size fish occurred at the temperature giving a balance between Apc (reflecting GEfeed) and Acmax (reflecting MSgrowth), and that temperature increased with fish size. (We encourage the reader to explore these complex relationships by accessing and running GEfeed&WvsTa.stm.)

In the preceding consideration of GEfeed and fish weight effects on the relation between red drum growth and temperature, we have been careful to qualify the temperature as "constant." This is because Ecophys.Fish acclimates to temperature (and to DO), and therefore might be expected to respond differently to time-varying vs. time-constant regimes of temperature (and/or DO).

We explored the consequences of diel variation in temperature and DO on growth under Ecophys.Fish. Both because life at higher temperature makes greater demands on the oxygen resource for support of routine metabolism and because routine metabolism is limited by low DO, our expectation was that growth would be favored by the normal polarity of diel Ta and DO cycles; i.e., fish that experience daily highs in Ta and DO at the same time should grow faster than if the Ta and DO extremes were shifted out of phase. When the Ta and DO time-series observed in the 13-month-long PT04 trial were shifted relative to one another by 16 h, so that the Ta and DO cycles were maximally out of phase (i.e., maximum daily temperature corresponding with minimum daily DO, on average), Ecophys.Fish produced a terminal fish weight that was less than that simulated without any phase shift, as expected, but the difference was only 2% (1,462.5 g under PT04OptWinMMSO.stm vs. 1,433.2 g under PT04OptWinMMSO-16hDOShift.stm). Close examination of the Ta and DO series, and of the model outputs, suggested that the difference would have been greater if the average amplitude of the Ta and DO cycles had been greater and if their periodicity had been more regular.

To evaluate the latter circumstances, we used Ecophys.Fish to analyze a hypothetical regime of diel Ta and DO. We simulated an 8-week growth trial with red drum having initial weights of 10 g and subjected to perfectly regular "saw-tooth" cycles of Ta between 22 and 32°C and DO between 2 and 7 mg/L, each with a 24-h period. Results from the in-phase simulation were compared with those from a simulation with the DO series shifted 12 h, so that it was perfectly out of phase with the Ta series. The in-phase simulation produced a final fish weight substantially greater than the out-of-phase simulation. How much greater depended on what the simulated red drum were fed: In-phase fish fed ad libitum on 1,000-cal/g feed finished the trial about 27% larger than their out-of-phase counterparts (26.2 g vs. 20.7 g; DielCycle-0hShift.stm); the advantage increased to 67% when GEfeed was 4,000 cal/g (177.5 g vs. 106.4 g; DielCycle-12hShift.stm).

But the real surprise came when the cyclic-environment simulations were compared with otherwise identical ones in which Ta and DO were held constant at their minimum,

Table 3

Weight after 8 weeks for simulated red drum, initially weighing 10 g, fed 1,000- or 4,000-cal/g feed and subjected to "saw-tooth" diel cyles of temperature (Ta) between 22 and 32°C and DO between 2 and 7 mg/L, or to temperature and DO held constantly at the minimum, mean, or maximum values of the cycles. Results generated under DielCycle-0hShift.stm and DielCycle-12hShift.stm

	Final Fish Weight (g)	
Temperature/DO Treatment	GEFeed = 1,000 cal/g	4,000 cal/g
Cyclic, Ta and DO in phase	26.2	177.5
Cyclic, Ta and DO out of phase	20.7	106.4
Ta = 32, DO = 7	20.0	70.8
Ta = 27, DO = 4.5	29.4	78.3
Ta = 22, DO = 2	38.9	42.2

mean, and maximum values (Table 3). For simulations in which GEfeed was 1,000 cal/g, the growth of cycled fish was intermediate to that of fish held at constant values of Ta and DO equal to the extremes of the cycles. But for simulations in which GEfeed was 4,000 cal/g, the growth of cycled fish—whether or not Ta and DO cycles were in phase—far exceeded that of fish held under the best of the three sets of constant conditions (Ta = 27°C, DO = 4.5 mg/L). The in-phase cycled fish ended the simulated trial more than twice the size of its counterpart kept in the "optimum" regime of constant temperature and constant DO (Table 3). The explanation of out-performance on the part of cycled fish was that their values of MSgrowth were higher—not because their values of Mrtn were lower, as McClaren's "energy-bonus" hypothesis (McClaren, 1963; Brett, 1971) might suggest—but because their values of Mact were higher! They had higher values of Mact because exposure to the cyclical DO regime lowered their DOaccl states, in effect giving them more metabolic capacity than their counterparts exposed to constant temperature/DO regimes. The cycled fish fed the 1,000-cal/g feed also had increased metabolic capacity—but lacked access to the feed-energy substrates that would have enabled them to take full advantage of it.

If these responses of Ecophys.Fish reflect those that occur in real fish, they must be wildly exaggerated in the model—else we surely would already have known and exploited them. But perhaps some of the model's emergent behavior will help the user to recognize subtle patterns in his/her own experience with real fish that have resisted resolution until now.

In the heading of this section, we placed the word "'Emergent"' inside quotation marks in recognition that the model produced some results that we found surprising—even shocking. But, in so far as we have been able to determine, this deterministic model has produced no result that really careful, astute intellectual analysis could not have anticipated in advance of simulation. That is, Ecophys.Fish does no magic tricks that do not yield to careful scrutiny.

Applications of Ecophys.Fish Without and Within: Use of the Model to Explore Relationships Beyond Autecology

If Ecophys.Fish is to meet our expectations, it must have utility for addressing issues at organizational levels both above and below that of primary interest to the autecologist.

To demonstrate that the model has some versatility in both directions, we probed issues that lie beyond the effects of environment on metabolism, bioenergetics, and growth of the individual fish. First, as an extension of issues raised in the preceding section, we explored the interacting dynamics of red drum metabolism and pond DO regimes. Next, we asked if Ecophys.Fish could help us understand observed effects of dietary fat saturation on red drum growth. Finally, we used Ecophys.Fish to ask how, specifically, the metabolic performance of fast-growing, growth-hormone-transgenic fish might differ from that of their normal counterparts.

Red Drum Metabolism and the DO Regime in Their Pond: Synecological Feedback

Previously, we established that under Ecophys.Fish certain cyclical diel regimes of temperature and dissolved oxygen are expected to provide for greater growth of juvenile red drum fed high-energy feeds than is any constant-temperature, constant-DO regime. But what if the fish themselves, through their use of oxygen, exert a load sufficient to cause change in the habitat's DO regime? Might this sort of feedback alter relationships so that what is optimum autecologically is not, synecologically?

To explore this possibility, we used Ecophys.Fish to simulate for dynamic diel DO balance in a hypothetical, 1-m deep culture pond with 0.1, 10, 25, 50, or 100 10-g red drum per square meter (and per cubic meter). Oxygen resupply in this virtual pond was consistent with the reoxygenation relationship developed by Thomann and Fitzpatrick (1982) for shallow, circulating waters:

reoxygenation rate constant (1/day)

$$= ((3.962^{*}V\hat{}0.5)/H\hat{}1.5) + ((1/H)^{*}(0.728^{*}W\hat{}0.5 - 0.317^{*}W + 0.0372^{*}W\hat{}2)),$$

where H is depth in meters, V is depth-averaged current speed in m/sec, and W is wind speed in m/sec. (We chose the Thomann-Fitzpatrick formula because it seemed sensible for aquaculture ponds being stirred mechanically.)

Using 2 m/sec for wind speed, 0.4 m/sec for depth-averaged current speed, and 1 m for mean depth gave 3/day as the reoxygenation rate constant. Dynamic DO was determined (by trial-and-error) at the end of successive 1-h intervals over one 24-h day, as that DO for which reoxygenation rate = rate of oxygen-uptake by n fish/m^2, each weighing W g:

$$3^{*}(DO0 - DO) = VO2^{*}n^{*}W^{*}(24/1000),$$

or

$$DO = DO0 - 0.008^{*}n^{*}W^{*}VO2.$$

Values of DO0 were the ordinates of the diel [2,7 mgO2/L] saw-tooth regime used in the simulations described in the preceding section. Obviously, we were thinking of some idealized system in which the interplay of photosynthesis and respiration in the microbial community gives rise to a saw-tooth pattern. But we emphasize that the causal origin of this null regime is immaterial—except that its dynamic balance must be independent of fish activities other than oxygen-uptake (to keep what follows computationally tractable).

The model was executed both with an in-phase diel [22, 32°C] saw-tooth regime of temperature and with temperature constantly at the midpoint of the cycle, 27°C. In each case, stable temperature and DO acclimation regimes were achieved by trial-and-error manipulation of starting DOaccl and Taccl values until they were about the same as the corresponding values at the end. Simulated red drum were 10 g and were fed ad libitum on 4,000 cal/g feed. MMSO was 0.31, salinity was 10 ppt, and pH was 8.0.

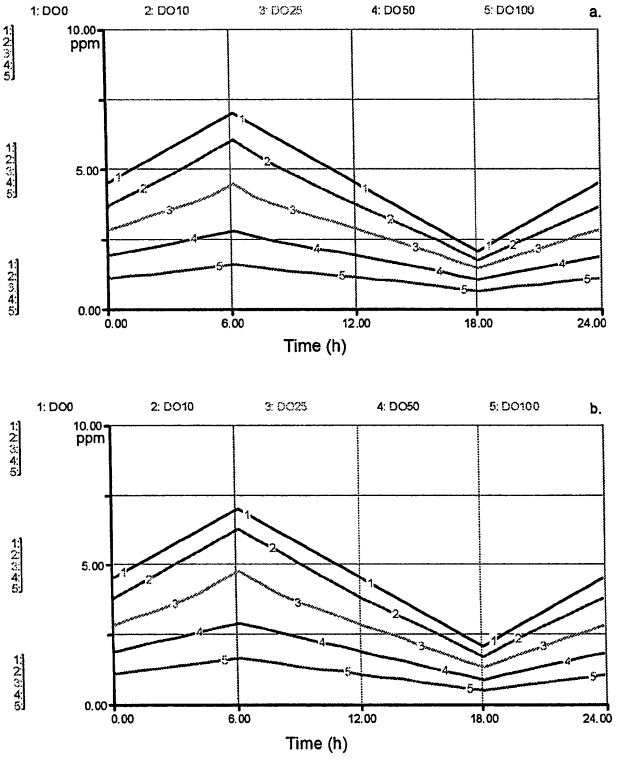

Figure 23. Simulated pond DO for loading densities of 0, 10, 25, 50, and 100 10-g red drum per square meter, in a 1-m-deep pond with the ambient DO regime indicated by DO0 and with an in-phase [22, 32°C] saw-tooth, diel cycle of temperature (a; RDPondTaCycle.stm) or with temperature constantly at 27°C (b; RDPondTa27.stm), under the nominal red drum model. Consider the time axis to extend from noon on one day until noon on the next. See text for DO-balance model.

The pattern of pond DO was similar for cyclical- and constant-temperature regimes (Figures 23a and 23b; RDPondTaCycle.stm, RDPondTa27.stm): As the fish-biomass density increased, pond DO was depressed—but that depression was progressively damped as the native DO cycle (DO0) approached its minimum. The reason was that more fish tended to use more oxygen, but that use was limited by low DO. So the picture emerging at high fish densities was one of the fish "regulating" pond DO. Of course, all that really was happening, autecologically, was that individual fish curtailed their use of oxygen as DO fell below the limiting level.

Logically, the above result would have been expected under any reasonable model of cyclical habitat DO appropriately coupled with oxygen uptake by the fish. But beyond reasonable expectation, was that the optimum level of biomass loading for growth of individual fish (and not just the optimum for biomass production by the group), was a level well above zero (Figures 24a and 24b): For the cyclical-temperature regime, growth rate was maximum at 10 fish/m^2 (100 g/m^2); for the 27-°C regime, the optimum biomass density was even greater, 25 fish/m^2 (250 g/m^2). The explanation of this result is that optimum biomass densities reduced habitat DO to the degree that DOaccl was lowered, but not to the degree that DO fell (much) below DOlim—consequently, Mact and thus MSgrowth

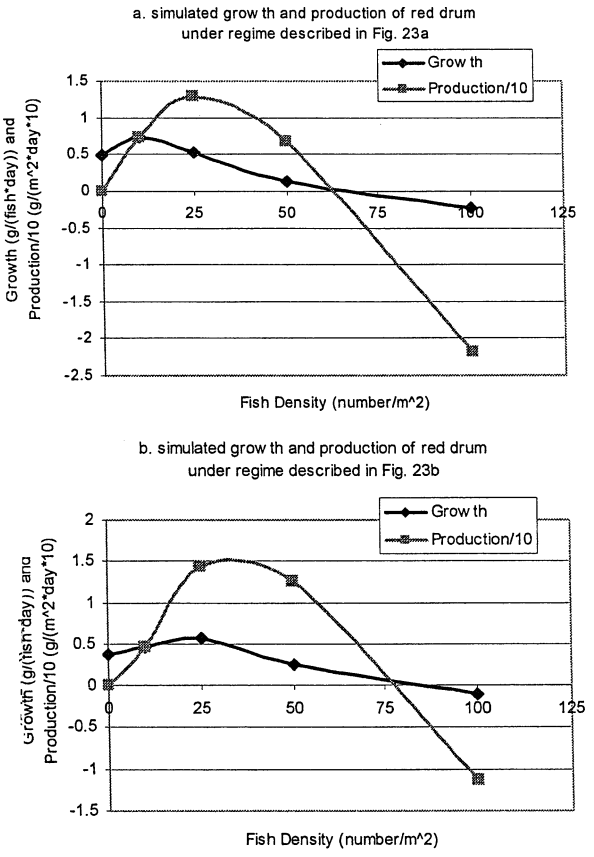

Figure 24. Simulated growth and production of 10-g red drum at loading densities of 0.1, 10, 25, 50, and 100 fish per square meter, in a 1-m-deep pond with the DO and temperature regimes described in Figures 23a (a) and 23b (b), under nominal red drum model (a, RDPondTaCycle.stm; b, RDPondTa27.stm).

were maximized. Under the constant-temperature regime, DO had to fall even lower before DOlim was compromised.

What a neat result (if real)! It means that aquaculturists actually may benefit from lower DOs in their culture systems. The caveat, of course, is that biomass loading to levels suggested by Ecophys.Fish as optimum, leaves little room for downside moves of the native DO regime (occasioned, for example, by calm, cloudy weather).

The apparent efficiencies of feed and oxygen use for production (Table 4) paralleled the patterns of growth rate vs. biomass density (Figures 24a and 24b). Simulated oxygen efficiency, at the optimum biomass density, was only about half the value we computed for the catfish *Clarias lazera* from data reported by Hogendoorn (1983) (see also Jobling, 1985), but well within the 1 to 10 gBiomassGain(wet)/gO2 range suggested by consideration of the theoretical costs of tissue biosynthesis and assembly (Atkinson, 1977). Simulated feed efficiency was somewhat higher than the 0.5 to 1.0 gBiomassGain(wet)/gFeed(as fed) values that we typically have observed in feeding trials with juvenile red drum. But in those trials,

Table 4

Efficiencies of production for 10-g red drum at loading densities of 0.1, 10, 25, 50, and 100 fish per square meter, in a 1-m-deep pond with the DO and temperature regimes described in Figures 23a and 23b, under nominal red drum model (RDPondTaCycle.stm and RDPondTa27.stm)

Fish Density (number/m^2)	Efficiency of Production			
	O2 Efficiency (gFish/gO2)		Feed Efficiency (gFish/gFeed)	
	Ta Cyclic	Ta Constant	Ta Cyclic	Ta Constant
0.1	2.37	1.99	1.14	1.03
10	3.20	2.37	1.31	1.13
25	2.50	2.79	1.15	1.22
50	0.82	1.51	0.59	0.87
100	−1.99	−1.00	–	−1.60

what we have measured is feed presented to the fish—and not necessarily feed consumed by the fish.

Metabolism and Growth of Red Drum Vs. Composition of Their Dietary Lipids

Craig et al. (1995) fed juvenile red drum prepared feeds with the lipid component manipulated to achieve varied characteristics, especially the kind and degree of fatty acid unsaturation. This 6-week feeding trial was conducted in two recirculating tank systems, one at 5 ppt and the other at 32 ppt salinity, following general protocols like those described above for the parameterization trials. Temperature was 27 ± 2°C. The fish started the trial with a mean weight of 3.25 g. The dietary lipid treatments were coconut, corn, menhaden, and hydrogenated menhaden oils at 7.0% of the dry diet, and menhaden oil at 14.0% of the dry diet. The coconut oil diet provided relatively high levels of 12- and 14-carbon saturated fatty acids, the corn oil diet provided relatively high levels of 18:2(n-6) monounsaturated fatty acids, and the menhaden oil diets provided relatively high levels of n-3 ("omega-3"), highly unsaturated fatty acids. The diet with hydrogenated menhaden oil permitted assessment of the relative roles of fatty acid saturation and chain length. The base diet was constructed to be marginally adequate in essential fatty acids. Measured responses included growth rate, proximate composition of fish tissues, and cold tolerance.

Here, the focus is on the growth response. Craig et al. (1995) observed no significant difference between salinity treatments, although for each of the five diet treatments the mean weight gain at 32 ppt was numerically less than at 5 ppt. The diet treatments themselves resolved into three statistical groups: 1) greatest growth—7% menhaden oil, 14% menhaden oil; 2) intermediate growth—saturated 7% menhaden oil, 7% corn oil; and 3) least growth—7% coconut oil. We asked, "How can we alter Ecophys.Fish to capture the effect of dietary lipid on growth of juvenile red drum?" Our essential clue came from the work of McKenzie et al. (1999), who showed that Adriatic sturgeon (*Acipenser naccarii*) fed a diet enriched with hydrogenated coconut oil had standard and routine metabolic rates 33 and 30% higher, respectively, than those fed a diet enriched with menhaden oil. With this information, we refined our question, asking, "Can we account for the red drum growth differences observed by Craig et al. (1995) by invoking diet-dependent differences in the model's fundamental

Table 5

Simulated vs. observed effects of dietary-lipid treatment on weight gain of juvenile red drum (mean initial weight, 3.25 g) at two salinities, 5 and 32 ppt, during a 6-week laboratory feeding trial. Simulated fish (FatSteve.stm) all had MMSO = 0.300 mgO2/(L*h), and differed (in parameters) only in their values of Smino, the fundamental intercept of standard metabolic rate. Observed values (means) of Wgain are from Craig et al. (1995); values with the same letter to right of bracket did not differ at alpha = 0.05

Dietary Lipid Treatment	Envir. Salinity, ppt	Modeled			Observed	
		Smino, mgO2/(g*h)	Mstd, mgO2/(g*h)	Wgain, %Wo	Wgain, %Wo	
Coconut 7%	5	0.111	0.267	243	246	c
	32	0.111	0.268	240	228	
Sat. Menhaden, 7%	5	0.106	0.243	343	369	b
	32	0.106	0.244	338	299	
Corn, 7%	5	0.106	0.243	343	341	b
	32	0.106	0.244	338	337	
Menhaden, 7%	5	0.100	0.216	491	496	a
	32	0.100	0.217	485	461	
Menhaden, 14%	5	0.100	0.216	491	463	a
	32	0.100	0.217	485	443	

intercept of standard metabolism, Smino? If so, does the model with requisite differences in Smino give differences in simulated Mstd consistent in direction and magnitude with those observed by McKenzie et al. (1999) for sturgeon?" The short answer to both questions, is, "Yes."

We began by adjusting Ecophys.Fish's MMSO to give a good fit for the mean-growth response of red drum fed the 7% and 14% menhaden oil diets at 5 ppt salinity; the required value was 0.30 mgO2/(L*h). Then, with MMSO set to 0.30, we adjusted Smino to fit the growth response for each of the other two diet treatment groups at 5 ppt. Finally, we used the same values of Smino to simulate growth at 32 ppt. Table 5 compares simulated results (FatSteve.stm) with those observed by Craig et al. (1995). Smino increased from its nominal value, 0.100 mg/(g*h) for the menhaden oil diets; to 0.106 mg/(g*h) for the corn and saturated menhaden oil diets; to 0.111 mg/(g*h) for the coconut oil diet. Terminal values of Mstd (and Mrtn, given that Mrtn = Winberg*Mstd = 2*Mstd) increased 23.6%, from the menhaden oil treatments to the coconut oil treatment. For every diet group, simulated weight gain was slightly less at 32 ppt than at 5 ppt salinity.

How to Make a "Super" Red Drum: Using Ecophys.Fish to Explore the Metabolic Basis of Performance Differences Between Normal and Growth-Hormone-Transgenic Fish

Working at a commercial aquaculture facility, Stevens et al. (1998) compared metabolism and growth of normal vs. growth-hormone-transgenic Atlantic salmon (*Salmo salar*). Under similar environmental conditions, the transgenic fish had routine metabolic rates (adjusted for weight differences) that were about 60% greater and weight-specific growth rates (over

the weight range, 6–45 g) that were two to three times those of their normal counterparts. The value of DO at which the fish lost attitudinal equilibrium (1.6–1.9 mgDO/L) and the critical swimming speed (4.3–4.8 body lengths per second) were similar between control and transgenic salmon. The authors judged the limiting oxygen concentration for routine metabolism (LOCr) to be less for the control fish (4 mgO2/L) than for the transgenic fish (6 mgO2/L), but applying the algorithm of Springer and Neill (1988) to their Figure 3 (data transcribed here, in our Figure 25b) suggests no difference or a somewhat lesser difference.

We manipulated the red drum version of Ecophys.Fish in an attempt to mimic the relative responses observed by Stevens et al. (1998). Mainly what we sought was some reasonable set of changes in the parameters of Ecophys.Fish that would generate the relative increases in routine metabolism and growth observed by Stevens and his colleagues for normal vs. transgenic salmon.

To our reasonable satisfaction, we succeeded (Figures 25a–f). The required adjustments were only three: 1) Smino increased, from the nominal normal value, 0.10, to 0.12 mgO2/(g*h), for our "transgenic" red drum; 2) Winberg increased from the nominal normal value, 2.0, to 2.4, for our "transgenic" red drum; and 3) MMSO increased, from the nominal normal value, 0.31, to 0.50 mgO2/(L*h), for our "transgenic" red drum. Our interpretation of these changes is that a growth-hormone-transgenic fish might have 20% more metabolic overhead, but have over 60% more metabolic capacity.

The Place of Ecophys.Fish Among Models of Fish Performance

The fundamental strength of Ecophys.Fish is its capacity to transform information about temporally varying physicochemical environment into fish growth rates; to accommodate in this process the residual effects of total environment, measured via short-term respirometric assays; and, to do all this in a way consistent with broad understanding of fish physiology and bioenergetics. The interactions of temperature and dissolved oxygen are represented in a functional way. And, for the first time, temperature and oxygen acclimation have been incorporated in a model of fish performance.

The central weakness of Ecophys.Fish is that it is only an autecological model, and, as such, it is poorly equipped to interact with the surrounding biotic world. Ecophys.Fish forages only in the crudest sense (it eats all the "food" it can get and process, all of the time), and it does not try at all to avoid becoming something else's food. This is to say, Ecophys.Fish is not a foraging or a predator-prey model, of the type into which the landmark bioenergetics model of Kitchell et al. (1974) has evolved, over several generations of successors (Kitchell et al., 1977b; Rice et al., 1983; Rice and Cochran, 1984; Hewitt and Stewart, 1989; Brandt and Hartman, 1993; Rand et al., 1997; Mason et al., 1998; Burke and Rice, 2002). Nor is Ecophys.Fish focused on establishing more thermodynamically reasonable expressions for the components of metabolism (Claireaux et al., 2000) or on energy-budgeting implications of changing biogeometry as the animal grows (Ursin, 1967; Kooijman, 2000).

Rather, Ecophys.Fish is the complement to all of these. We have gone to some lengths to demonstrate that our model can connect with levels of organization both below and above those of the individual fish. We hope that scientists who work at all three levels will use and improve the model.

Conclusion

Empirical estimation of MMSO, as performed in the bluegill study and in the CPL trial with red drum, removes the one "fudge factor" from application of the ecophysiological model.

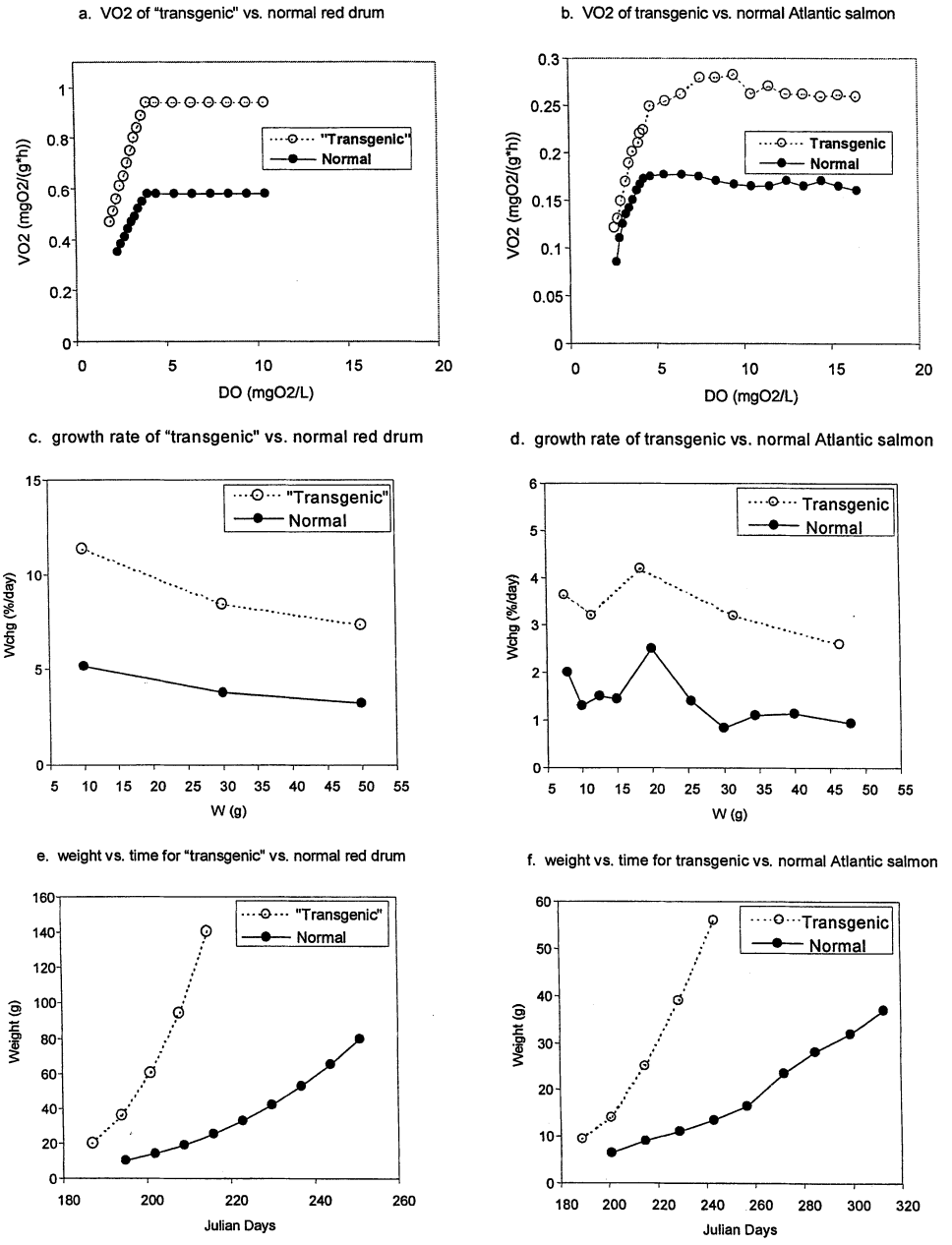

Figure 25. Comparisons of relative rates of routine metabolism and growth, for simulated "transgenic" vs. normal red drum (a, c, e; Transgenic.stm), with that observed by Stevens et al. (1998) for transgenic vs. normal Atlantic salmon (b, d, f). The salmon values in panels b, d, and f are from Stevens et al. (1998) Figures 3a, 1b, and 1a, respectively.

It thus permits an objective criterion of habitat suitability for fish performance, in terms of potential growth rate, based solely on environmental time-series and on respirometry with samples of fish and water from the habitat—without the need to monitor growth of fish. Put another way: With samples of fish, water, and environmental data, one might use the ecophysiological model in conjunction with respirometric assays to find MMSOs that would constitute a measure of habitat value for performance of fish. This measure would be largely independent of ephemeral variation in the ordinary abiotic components of environment (i.e., temperature, DO, salinity, and pH), instead reflecting differences in more refractory aspects of habitat quality. If it can be assumed or established empirically that forage—more correctly, amount and caloric yield of food—is not limiting, then MMSOs potential dependency on nutritive status also is eliminated, and MMSO becomes a measure of what one might label "intrinsic" habitat quality. Or, perhaps the label "residual" habitat quality is a better choice.

With MMSO estimates in hand, it becomes a simple matter to use Ecophys.Fish to explore "what if" scenarios. What if temperature increased 1°C across all habitats? What if high-energy, artificial feed were provided? What if nighttime DOs were elevated by aeration? Is there a growth penalty associated with maintaining a too-stable environmental regime?

But how robust and reliable would one expect the answers to such questions to be? Regrettably, we don't have a confident answer to that larger question. In the case of red drum, we have a version of Ecophys.Fish that is well grounded in parameterization experiments—but we have had little experience so far in using it with empirically estimated values of MMSO. In the case of bluegill, the opposite situation obtains: All our experience has derived from attempts to use Ecophys.Fish with values of MMSO measured via respirometry—but the model itself was developed without the benefit of parameterization trials. So with red drum, we really can't be sure the required values of MMSO (required to fit growth data) will be the same as those delivered via respirometric assay—although the few paired data we have generated so far are encouragingly congruent (Figure 16b). And with bluegill, either that version of the ecophysiological model is seriously flawed (because it produced simulated values of bluegill Wchg three times the observed values, when Wchg was large—despite the fact that observed Wchg and MMSO were highly correlated) or we were victimized by a too-casual set of feeding protocols.

Obviously, improved answers will require more work. All future cage trials need to be accompanied by respirometric assays of marginal metabolic scope. Cage trials should be designed to encompass contrasting environments ("good" and "bad" habitats). Any feed provided to caged fish should "match the hatch;" i.e., fish should be fed a feed that has the same palatability, digestibility, and gross energy content as the natural forage accessible to the fish. And, before there is any attempt to use Ecophys.Fish to interpret cage trials in the field (under variable environmental regimes), parameterization trials in the lab should be performed—with temperature and dissolved oxygen at a minimum.

Here are some additional areas in which Ecophys.Fish really needs help in a more fundamental and generic sense:

1. temperature and DO acclimation dynamics; salinity acclimation;
2. energy density dynamics (GEfish flux);
3. weight effect on feeding, feed-processing rates;
4. directive effects of temperature and DO on feeding; controlling effect of temperature on feed processing (independent of effects via metabolic scope);
5. interaction of nutrition and bioenergetics;

6. endocrine submodels for directive-factor space compression object; directive effects of photoperiod and other components of "season" on MMSO;
7. resolution of juvenile growth from larval development;
8. reproductive biology;
9. stochastization of component processes.

". . . Where do we go from here?" This was the title question raised by a 1992 symposium on fish bioenergetics modeling (Hansen et al., 1993). The participants' broad answer was, in part, onward to improved model components. And as our list above would indicate, we concur that models like Ecophys.Fish can never be really 'good enough.' But we view improvement in the functions and parameters of Ecophys.Fish only as necessary side trips (and, no doubt, even backtracks), not the main pathway to fundamentally better understanding of aquatic production systems. For that, we will need what Harte (2002) has called "a synthesis of the Newtonian and Darwinian worldviews":

> "Physicists seek simplicity in universal laws. Ecologists revel in complex interdependencies. A sustainable future for our planet will probably require a look at life from both sides."

Harte's contrast reminded us of the discussion by Grant et al. (1997), of ecological systems as systems characterized by 'organized complexity,' and the essential role of systems analysis and simulation in moving ecology toward the 'organized simplicity' of physics. Logically, the interface between ecology and physics must be (in part) the kind of biology represented in Ecophys.Fish.

Already, Neill has incorporated Ecophys.Fish into EcoFish, which is replete with presumptive lethal- and directive-factor components. EcoFish now serves up virtual subjects for simulated laboratory experiments conducted by undergraduate fish biology students at Texas A&M. Somewhere, sometime beyond Ecophys.Fish and EcoFish, we would hope there will come "EcoPop," "EcoPond," "EcoEstuary," etc. A potential, if rudimentary roadmap for this successional path is provided by Neill et al. (1994), who used Fry's (1947, 1971) "physiological classification of environment" to suggest patterns of mechanistic connection between levels of biological/ecological organization. A prime motivation for the development of Ecophys.Fish was to test our own preparedness to undertake the journey suggested by that roadmap. We hope our investment in Ecophys.Fish might make the larger journey less daunting for everyone else, too.

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